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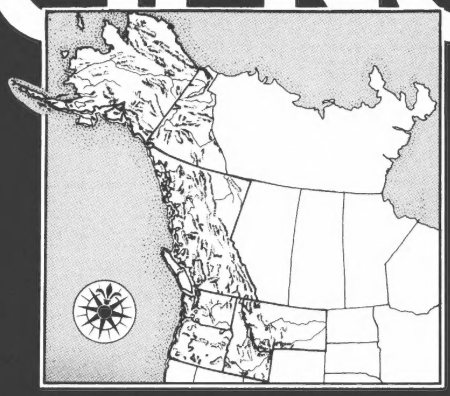
NORTHWEST SCIENCE



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Tolerance of Seedlings of Ponderosa Pine, Douglas-fir, Grand Fir, and Engelmann Spruce for High Temperatures

Abstract

The heat tolerance of 2- to 4-week old seedlings of ponderosa pine (*Pinus Ponderosa* Dougl. ex Laws.), Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco), grand fir (*Abies grandis* (Dougl. ex D. Don) Lindl.), and Engelmann spruce (*Picea engelmannii* Parry ex Engelm.) was determined and compared by exposing them to various time-temperature combinations in a "dry water bath" apparatus. Isosurvival curves indicating the time-temperature combinations that resulted in approximately equal survival were constructed for each species. Small (2 to 4°C) but significant differences in heat tolerance were found among species with ponderosa pine having the greatest tolerance and Engelmann spruce the least. Douglas-fir and grand fir were generally intermediate in heat tolerance.

Introduction

Mortality of natural regeneration during the first growing season is common on many clearcut and shelterwood units in central Oregon because of high soil surface temperatures. Although the lethal high temperature range for tree seedlings as related to time of exposure has been established in general (Baker 1929, Lorenz 1939, Shirley 1936), there is considerable variation in results because of the variety of experimental methods used. Because comparisons of the heat tolerance of coniferous species in the Pacific Northwest are scarce (Minore 1979), more specific information is needed on the time-temperature relationships of major species. Such information could be used with data on soil surface temperature obtained in regeneration units to better evaluate causes of seedling mortality.

The purpose of this investigation was to estimate and compare the relationship between seedling survival and time of exposure to high temperatures for ponderosa pine (*Pinus ponderosa* Dougl. ex Laws.), Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco), grand fir (*Abies grandis* (Dougl. ex D. Don) Lindl.), and Engelmann spruce (*Picea engelmannii* Parry ex Engelm.).

Materials and Methods

Seedlings and Soil

Seeds of Douglas-fir, grand fir, and Engelmann spruce were obtained from the USDA Forest Service Wind River Nursery, Gifford Pinchot National Forest. These seeds were originally collected in the Mount Hood National Forest (Barlow and Bear Springs Ranger Districts) at an elevation of about 1100 m. Seed from ponderosa pine was collected in the Pringle Falls Experimental Forest, at an elevation of about 1500 m. Soil used in these tests came from the upper 25 cm in the Experimental Forest. This soil is a well-drained Regosol developing on Mazama pumice.

Experimental Design and Procedure

The experiment was a completely randomized design with a 6 x 8 factorial arrangement of treatments for each species. Six temperatures and eight exposure times were used. The temperatures tested were 48.9, 51.7, 54.4, 57.2, 60.0, and 62.8°C (120, 125, 130, 135, 140, and 145°F); the times of exposure were 1, 5, 10, 20, 30, 60, 180, and 300 minutes. Each of the 48 treatment combinations was replicated twice.

Seeds were germinated in vermiculite, and ten germinated seeds (radicle 1 to 2 cm long) were planted in the Mazama pumice soil in rectangular boxes (30 x 6 x 12 cm) in a single row about 3 cm apart. Boxes were placed in a greenhouse and seedlings grown for 2 to 4 weeks at a 24 to 32°C day and 6 to 10°C night temperature regime, with a 15-hour photoperiod. During this period, the soil was well watered and seedlings did not experience water stress. Seven to ten seedlings were present in each box when treatments were

applied from March through June 1981. Batches of seed were germinated at various times during this period so all seedlings were 2 to 4 weeks old when treatments were applied.

Heat was applied directly to the lower stem of the seedlings by means of the "dry water bath" technique developed by Silen (1960) (Figure 1). Copper tubing connected to a circulating immersion heater in a water bath was placed on both sides of the seedlings and pressed firmly against the seedlings with clamps. No visible seedling damage was observed from use of the clamps. A thermometer in a copper tube attached to the tubing next to the seedlings was used to measure the temperature at the base of the seedlings.

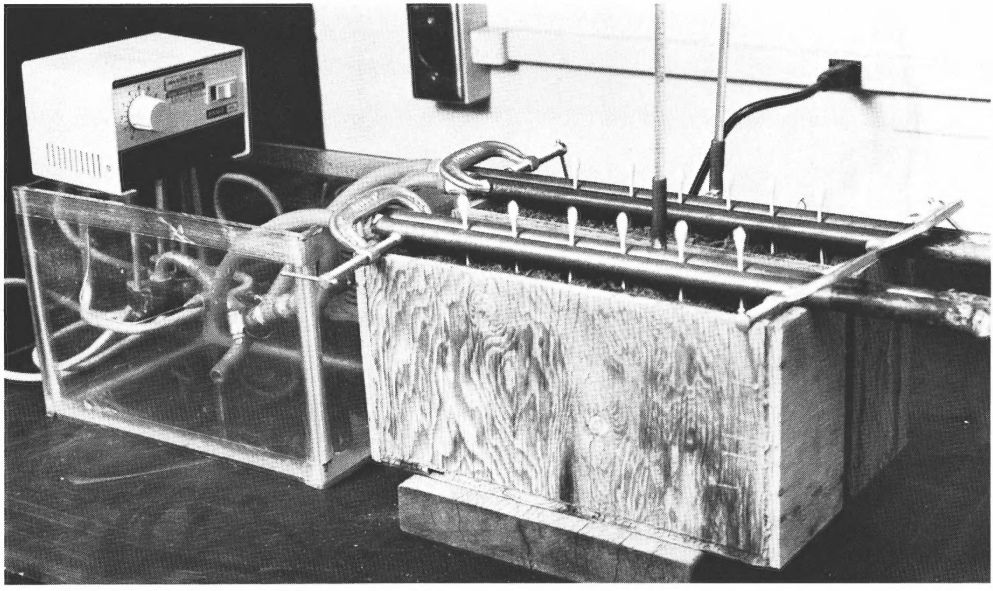

Figure 1. "Dry water bath" apparatus. Water is circulated from water bath by immersion heater through copper tubing that surrounds seedlings (represented by q-tips).

After seedlings in each box received a specific time-temperature treatment, they were returned to the greenhouse. In November 1981, the number of surviving seedlings in each replication was counted and the results expressed as a survival percentage. Because of the many treatment combinations that resulted in 100 or 0 percent survival, a standard two-way analysis of variance to test the time-temperature interaction was not appropriate. To illustrate the effect of time and temperature on survival, observed means of each treatment were plotted as a three-dimensional graph for each species. Isosurvival curves that estimated the time-temperature combinations resulting in survival of 10, 30, 50, 70, and 90 percent of the seedlings were constructed for each species using curvilinear equations of the form:

$$Y = a + b(1 - e^{-cx})^d;$$

Where Y = temperature, x = time, and a, b, c, and d are regression coefficients. To develop these curves, percentage of survival was regressed on temperature for each time period. The time-temperature data for each survival percentage (10, 30, 50, 70, and 90) was then obtained by reading the temperature at the point where each time curve intersected the survival percentage abscissa. To test for differences in heat tolerance among species, a single average isosurvival curve was constructed for each species and then converted to linear form by a logarithmic transformation of time. These linear curves were

tested for significant differences in slope or level to determine differences among species.

Results and Discussion

Both the temperature to which seedlings were exposed and the length of the exposure had pronounced effects on seedling survival for all species (Figures 2-5). It was evident that time and temperature interact strongly to affect seedling survival. For ponderosa pine, for example, an exposure time of 180 minutes at a temperature of 48.8°C resulted in the same survival (100 percent) as an exposure time of 1 minute (Figure 2). But exposure to a temperature of 54.4°C resulted in 100 percent survival after 1 minute and only 15 percent survival after 20 minutes. The effect of different temperatures at a constant time was equally dramatic. After 1 minute of exposure there was about a 20 percent drop in survival as temperature was raised from 48.8 to 57.2°C. When seedlings were exposed for 20 minutes, however, survival decreased from 87 to 0 percent within the same temperature range, with most of the mortality occurring at 54.4°C.

The response of ponderosa pine and Douglas-fir to the treatments was similar except survival of ponderosa pine was generally higher at 48.8 and 51.8°C (Figures 2 and 3). No seedlings of either species survived temperatures of 54.4°C or higher when exposed for 30 minutes or longer.

Grand fir and Engelmann spruce seedlings were generally less tolerant of high temperatures than were ponderosa pine or Douglas-fir. More treatment combinations resulted in no survival (Figures 4 and 5).

Using the basic time-temperature survival data, a series of isosurvival curves were calculated for each species to show seedling survival within the range of times and temperatures used in this study (Figure 6). The curves illustrate the negative exponential relationship existing between time and temperature and show that a short period of high temperature resulted in the same survival rate as a longer period at a lower temperature. As time of exposure increased from 0 to about 15 minutes, the temperature that a seedling could tolerate decreased dramatically. At longer exposures (over 60 minutes), the effect of time was less important in seedling mortality. I estimated, for example, that about 30 percent of Douglas-fir seedlings would survive a temperature of 57.6°C for 4 minutes (Figure 6B), but at 60 minutes the temperature must be no higher than about 51.2°C to obtain the same rate of survival—a decrease of 6.3°C. When time of exposure increased from 90 to 300 minutes, however, the temperature to obtain a 30 percent survival rate only decreased from 50.8 to 50.0°C. Silen (1960) reports similar results for heat tolerance of 1-week-old Douglas-fir seedlings. About 30 percent of his seedlings survived a temperature of 60°C for 4 minutes, and a temperature of about 54.4°C for 60 minutes resulted in the same rate of survival. No time-temperature data were available for grand fir after 60 minutes because all of the treatment combinations resulted in zero survival (Figure 6C). These curves therefore have a linear form after 60 minutes in contrast to the more realistic gradual decrease in temperature with time of the other species.

The time-temperature isosurvival data are summarized in Table 1 for the four species for the 5- to 60-minute range. Ponderosa pine generally was able to withstand the highest temperatures at any exposure time, Engelmann spruce was the least tolerant. Differences of 2 to 4°C in heat tolerance were found between these species. Douglas-fir and grand fir were intermediate in their resistance to heat; they differed by only a fraction of a degree at some times and survival rates.

Statistical analyses of the average isosurvival curves showed there were significant differences ($P < 0.01$) in levels of the ponderosa pine and grand fir curves and between the ponderosa pine and Engelmann spruce curves. Levels of the Douglas-fir and spruce curves also differed significantly ($P < 0.05$); differences between Douglas-fir and grand fir curves were significant at the 10-percent level.

Based on this study, the relative heat tolerance of young seedlings of these species from highest to lowest is as follows: ponderosa pine $\cong$ Douglas-fir $>$ grand fir $\cong$ Engelmann spruce. Direct comparison with other studies is difficult because of differences in seed source, age of seedlings, and experimental technique, but ponderosa pine is considered to have a high degree of heat tolerance (Roeser 1932). These results agree with the distribution of these species within plant communities along an elevational transect on the east slope of the Cascade Range;

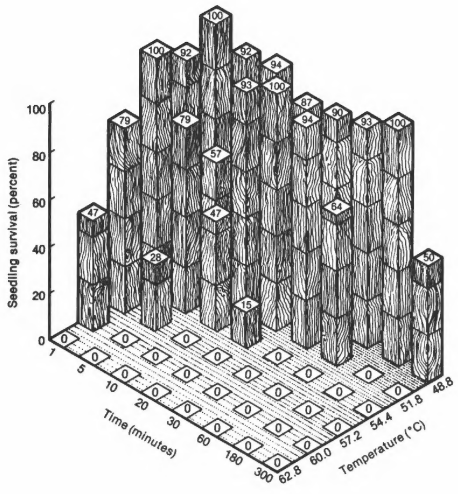

Figure 2. Effect of temperature and exposure time on survival of 2- to 4-week-old ponderosa pine seedlings. Numbers on tops of bars indicate survival percentages.

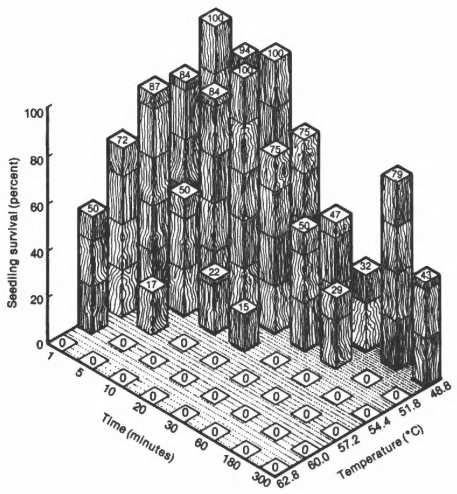

Figure 3. Effect of temperature and exposure time on survival of 2- to 4-week-old Douglas-fir seedlings. Numbers on tops of bars indicate survival percentages.

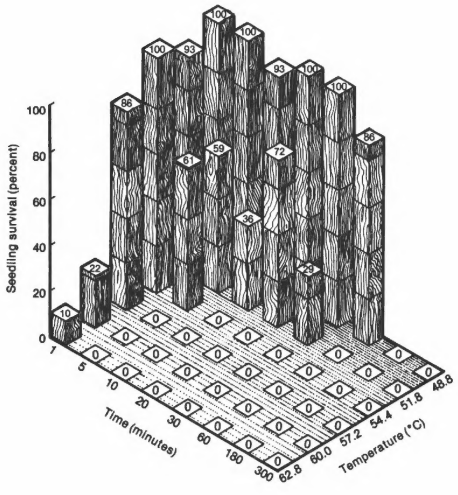

Figure 4. Effect of temperature and exposure time on survival of 2- to 4-week-old grand fir seedlings. Numbers on tops of bars indicate survival percentages.

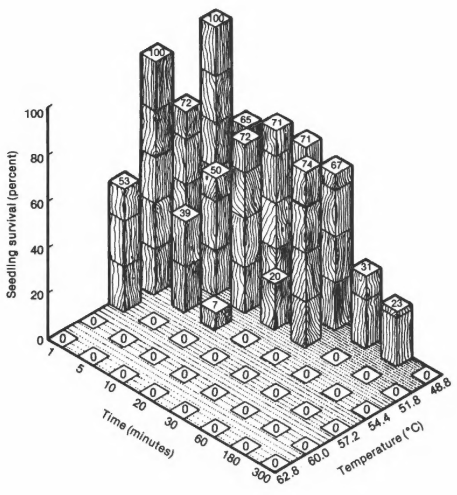

Figure 5. Effect of temperature and exposure time on survival of 2- to 4-week-old Englemann spruce seedlings. Numbers on tops of bars indicate survival percentages.

Figure 6. Isosurvival curves of 10, 30, 50, 70, and 90 percent for 2- to 4-week-old seedlings: (A) ponderosa pine, (B) Douglas-fir, (C) grand fir, (D) Engelmann spruce. Each curve gives estimates of the various time-temperature combinations resulting in equal survival.

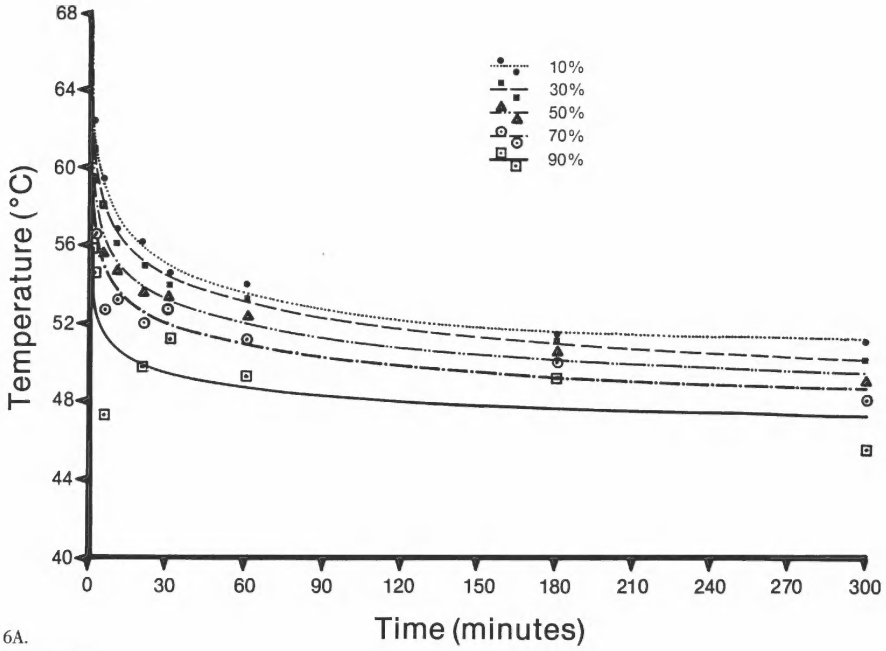

Figure 6A.

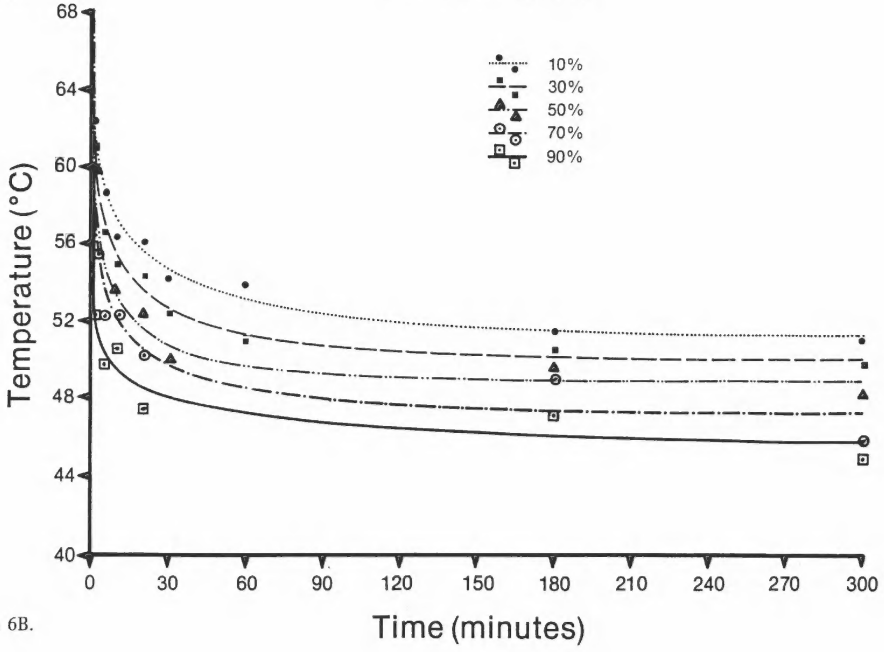

Figure 6B.

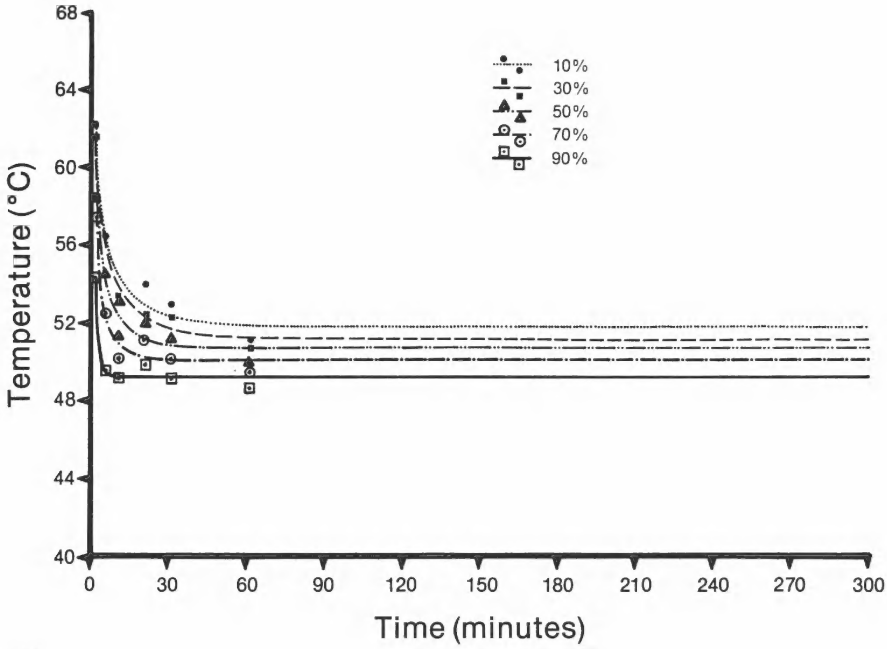

Figure 6C.

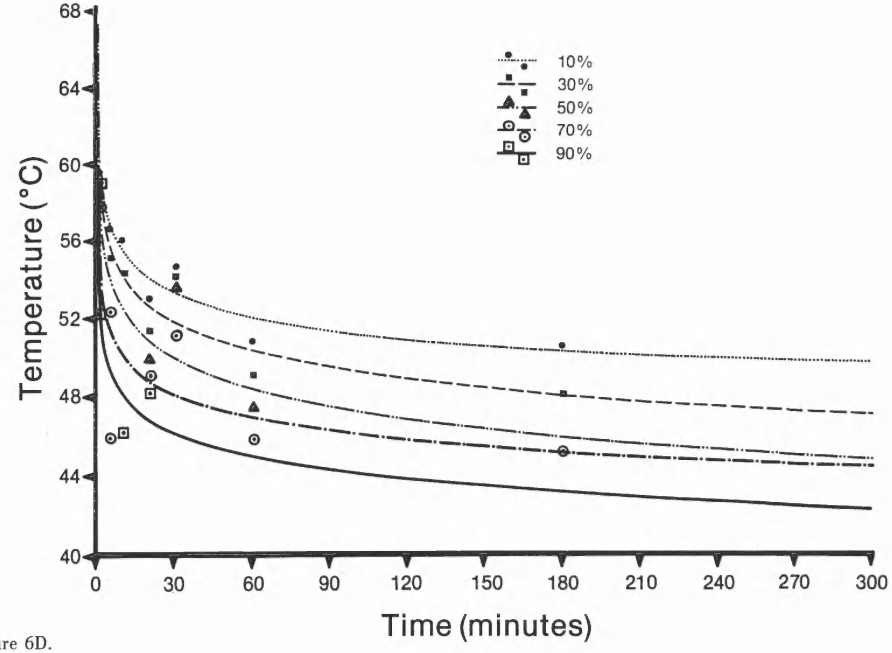

Figure 6D.

TABLE 1. Temperatures (°C) resulting in equal survival among four species at four time periods by percentage of survival.[1]

	10 percent survival	30 percent survival	50 percent survival	70 percent survival	90 percent survival
Ponderosa pine					
5 min	59.0	57.8	56.3	54.4	51.2
20 min	55.9	55.0	53.9	52.4	49.8
30 min	54.9	54.2	53.2	51.8	49.4
60 min	53.5	52.7	52.0	50.9	48.8
Douglas-fir					
5 min	58.4	56.8	54.8	53.3	50.2
20 min	55.4	53.6	51.5	50.3	48.5
30 min	54.5	52.6	50.8	49.6	48.0
60 min	53.0	51.3	49.7	48.4	47.3
Grand fir					
5 min	56.3	55.7	54.2	52.1	49.4
20 min	52.7	52.3	51.2	50.0	49.1
30 min	52.1	51.5	50.9	50.0	49.1
60 min	51.8	51.2	50.9	50.0	49.1
Engelmann spruce					
5 min	56.8	55.4	53.7	50.7	49.1
20 min	54.1	52.4	50.7	48.5	46.8
30 min	53.3	51.5	49.8	47.9	46.1
60 min	52.1	50.2	48.3	46.7	45.0

[1]Temperature values read from isosurvival curves.

ponderosa pine is found in warmer, low-elevation communities, and grand fir and Engelmann spruce occupy cooler, high-elevation sites.

It is apparent from these results, as well as those of earlier studies, that seedlings of many tree species suffer mortality from high temperatures within the range of about 48 to 68°C depending upon the length of exposure. In this study, the difference in temperature at a given time, resulting in equal mortality between the most and least resistant species (ponderosa pine and Engelmann spruce), was only 2 to 4°C. Although small, such differences were statistically significant and apparently confer a competitive advantage to establishment of ponderosa pine on warm, dry sites.

Obviously, the time-temperature relationships of these species as measured on single seed lots from specific geographic locations cannot be considered as representative of these species in all locations. Also, the response of seedlings to environmental factors in the greenhouse or growth chamber cannot be directly extrapolated to field conditions. Although the absolute degree of heat tolerance of each species may vary in response to different environmental conditions, it is reasonable to assume that the relative heat tolerance among these species will remain relatively unchanged with ponderosa pine retaining its advantage.

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Vegetation Colonizing River Gravel Bars in the Rocky Mountains of Southeastern British Columbia

Abstract

The vegetation of gravel bars in the Blaeberry River near Golden, B.C. was classified into six community types using six species-groups derived by Braun-Blanquet techniques. The distribution of communities on the bars appeared to be controlled by variation in soil texture and water table depth. Successional development of communities found in xeric and mesic locations led to a community containing species common to the climax floodplain forest of the area. Communities found in wet depressions may not be successionally related to other bar communities because of frequent inundation and sediment deposition.

Introduction

Primary successional plant communities form a significant component of the vegetation in mountainous regions because new land surfaces are continually being exposed by erosional forces. As early as 1916, Cooper described successional vegetation on morainal and glacial outwash materials and reports of similar research in glaciated areas are numerous (Crocker and Major 1955, Tisdale *et al.* 1966, Viereck 1966, Lawrence *et al.* 1974). Although most major river valleys in the Canadian Rocky mountains contain areas of alluvial gravel bars, the plant communities colonizing these areas and the factors controlling their establishment have not been studied. This paper describes the vegetation of gravel bars typical of those found in river valleys along the western slope of the Rocky mountains in southeastern British Columbia.

Study Area

The Blaeberry River runs southwest through the western ranges of the Rocky mountains to join the Columbia River 16 km north of Golden, B.C. The western ranges consist of sedimentary and metamorphic rocks, mainly limestone and quartzite, and are deeply dissected through glacial and stream erosion (Holland 1964). Outwash from alpine glaciers has been deposited along several sections of the Blaeberry valley to form networks of channels and bars. Our study site, situated at an elevation of 1900m asl (51° 34'N, 116° 48'W), is representative of a braided section of river 13 km in length.

The forests of the upper Blaeberry valley adjacent to the study site are dominated by Engelmann spruce (*Picea engelmannii*) and subalpine fir (*Abies lasiocarpa*) on the valley walls, and by white spruce (*Picea glauca*) and black cottonwood (*Populus trichocarpa*) on the flood plain. Bell (1971) placed the valley bottoms in the subboreal spruce zone and the upper slopes in the Engelmann spruce-subalpine fir zone of Krajina (1965). Rowe (1972) describes this part of the valley as Interior Subalpine Forest.

The closest meteorological station to the study site, Golden, B.C., averages 50 cm of precipitation annually with 40 percent falling as snow. January is the wettest month while April is the driest. Average monthly temperatures range from -11.6° C in January to 17.2° C in July, with seven months warmer than 0° C and 170 frost free days annually. The study site is higher in elevation and farther into the mountains than Golden and probably has lower temperatures and higher precipitation.

Methods

Fifty releves were located in homogeneous stands of vegetation which appeared, on the basis of initial site reconnaissance, to represent distinct communities on the bar complex. Plot dimensions were dictated by the size and shape of individual stands but were based on minimal area determinations in each of the reconnaissance community types.

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Each releve included a list of all species found in the plot rated for cover and abundance according to the seven point Braun-Blanquet scale. Local habitat conditions were described in terms of size and nature of the stand, surrounding vegetation, slope, microrelief, moisture regime, drainage, and estimated frequency of flooding. Pits were dug in each plot to examine soil texture, profile characteristics and water table depth. A voucher collection of all plant species recorded is on file in the Herbarium at the University of Victoria (UVIC).

Floristic data were analysed using the Table Method of Ellenberg (1956), facilitated by a computer program which performed the initial sorting (Ceska and Roemer 1971). A description of the Table Method is given by Mueller-Dombois and Ellenberg (1974).

Of the species groups generated by the computer program using different sorting rules, those which best reflected conditions on the bars were chosen. The selected groups were reorganized to indicate the dispersal of the community types along the prevailing environmental gradients using the program's rewriting mode. Final sorting of the data table was done by hand to emphasize relationships among community types.

Results and Discussion

Analysis of the floristic data produced four species groups (Table 1). In addition, two single species "groups" were recognized because of their value for differentiating community types. Named after the species dominant in each, they are the Carex, Juncus, Parnassia, Epilobium, Populus, and Dryas groups.

The species of the Carex group are most prevalent in wet areas but occur widely on the bar complex in locations with wet to mesic moisture regimes. The Juncus group is restricted in distribution to the wettest sites on the bars, often growing in silt deposits adjacent to standing water. The species of the Parnassia group are most often observed growing in moist sandy deposits along the sides of depressions and old river channels. The Epilobium group is widely distributed in sandy to gravelly areas with moist to mesic moisture regimes. The Populus group is restricted to stable areas in the center of bars where mesic conditions prevail. The Dryas group consists of a single species, *Dryas drummondii*, which forms extensive mats in xeric, gravelly locations.

Six community types were differentiated on the basis of presence or absence of the species groups. The community types were named according to the dominant species group and edaphic characteristics as follows: the Carex Wet Depression, Parnassia Silt Channel, Parnassia/ Epilobium Deep Sand, Epilobium Shallow Sand, Populus Stable Bar, and Dryas Dry Gravel community types.

1. Carex Wet Depression Community Type

The Carex community type is characterized by the presence of the Carex and Juncus species groups and is dominated by *Carex oederi*, *Equisetum variegatum* and *Juncus alpinus*. Other commonly occurring species include *Deschampsia cespitosa, Salix farriea* and *Aster hesperius*. This type is found in depressions and old channels where fine sand and silt have accumulated. The depth to water table at the time of sampling averaged 27 cm (range 15-40 cm) ensuring that hygric conditions prevail throughout the year. Flooding of this community probably occurs annually when the water table rises in spring flood.

2. Parnassia Silt Channel Community Type

The Parnassia community type is characterized by the presence of the Parnassia and Carex species groups and partial occurrence of the Epilobium group. The dominant species are *Parnassia palustris, Carex oederi* and *Equisetum variegatum*. In addition to members of the species groups mentioned, *Salix farriae, S. wolfii, Aster hesperius, Prunella vulgaris, Calamagrostis inexpansa,* and *Juncus alpinus* may occur.

Communities of this type are commonly found along lower slopes and bottoms of old river channels which have become filled with silt and fine sand to depths of 20-25 cm. Water table depths average 46 cm (range 30-55 cm). This type often occurs around wet depressions occupied by the Carex type. Flooding probably occurs every 2-4 years, either as seepage from rising ground water or low velocity flow over the surface of the bar.

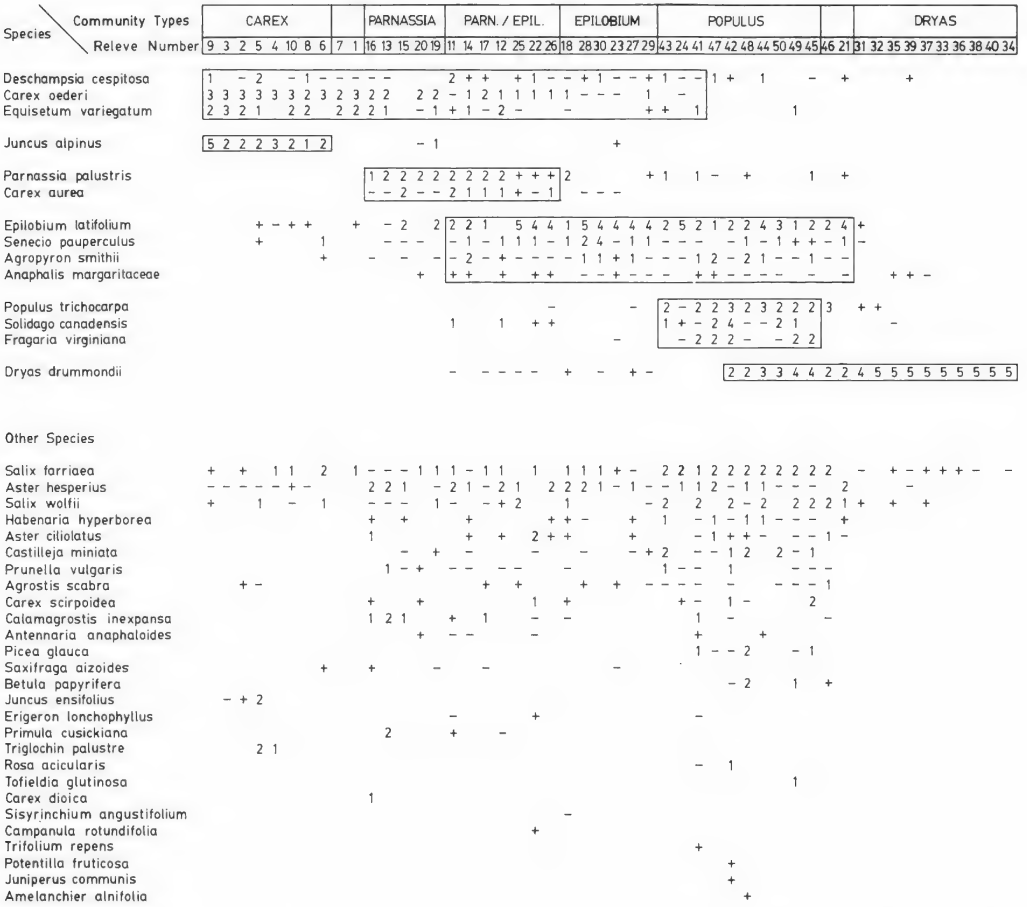

TABLE 1. Species/releve table showing derived species groups and community types. Species nomenclature follows Hitchcock and Cronquist (1973). Cover and abundance of each species in each releve were rated as follows: 5 = 75-100% cover; 4 = 50-75% cover; 3 = 25-50% cover; 2 = 5-25% cover; 1 = 1-5% cover; + = few, with low cover; − = solitary, with low cover.

3. Parnassia/Epilobium Deep Sand Commmunity Type

The Parnassia/Epilobium community type is characterized by the Parnassia, Epilobium, and Carex species groups and is strongly dominated by *Parnassia palustris* and *Epilobium latifolium*. Other species which may occur include *Salix farriea, S. wolfii, Aster hesperius, Prunella vulgaris, Solidago canadensis,* and *Dryas drummondii*. This type occupies old channel positions similar to the Parnassia type but the soil consists of 15-30 cm of coarse sand over gravel. Parnassia/Epilobium communities are often found in upper slope positions around depressions that support the Parnassia type.

4. Epilobium Shallow Sand Community Type

The Epilobium community type is characterized by the Epilobium and Carex species groups. *Epilobium latifolium* is strongly dominant. *Salix farriea* and *Aster hesperius* occur commonly while *Dryas drummondii, S. wolfii,* and members of the Parnassia species group may also be present. Communities of this type are found in shallow depressions and upper slope positions with an average water table depth of 45 cm (range 30-60 cm). The soil consists of a 2-8 cm layer of coarse sand over gravel. They often occupy positions between Parnassia/Epilobium communities on depression slopes and Dryas communities on the top of the bar.

5. Populus Stable Bar Community Type

The Populus community type is characterized by the presence of the Populus and Epilobium species groups. Two phases are distinguished by the presence of either the Carex or the Dryas species group. This community type is dominated by long lived woody perennials including *Populus tremuloides, Salix farriae* and *S. wolfii, Epilobium latifolium* is the dominant herbaceous species. Other commonly occurring species include *Aster hesperius, A. ciliolatus, Castilleja miniata, Habenaria hyperborea, Picea glauca,* and *Prunella vulgaris*.

This community type is generally found in the center of bars often where there is a slight rise or knoll. Water table depth averages 50 cm (range 40-60 cm). The soil consists of a layer of fine sand and silt 8-15 cm deep over gravel. The upper 1-3 cm of the silt layer is enriched with organic matter. In some locations the finer surface horizon appeared to have been deposited in the standing vegetation.

6. Dryas Dry Gravel Community Type

The Dryas community type is dominated entirely by *Dryas drummondii. Salix farriae, S. wolfii,* and *Anaphalis margaritaceae* occur occasionally. This community type is found on the tops of bars, mainly on the upstream end, where floodwaters have removed sand and silt leaving only coarse gravels. The water table depth of 60 cm and the coarse texture of the soil make these sites extremely dry. During flooding, this community type is exposed to the full force of the river current which can cause severe disturbance or destruction of the vegetation cover. The prostrate habit and woody stems and roots of *Dryas* make it well suited to such severe conditions. In addition *Dryas* has a symbiotic association with nitrogen-fixing organisms which undoubtedly increases its ability to colonize these infertile soils (Lawrence *et al.* 1974).

In addition to the six community types described, the data analysis generated two type fragments, one having affinities with the Carex and Parnassia communities and the other having affinities with the Dryas communities. These fragments could not be considered as separate community types because they were represented by only two releves each. It is not known whether these fragments are mere anomalies or if they represent infrequently occurring communities which would have been apparent in a more extensive survey of bars in the Blaeberry valley.

Distribution of Community Types

The Blaeberry River gravel bar communities appear to be distributed in relation to edaphic site conditions, particularly soil texture. Textural differences between locations on a bar arise through differential suspension and deposition of sediment during periods of flooding. Water flowing rapidly over the top of a bar will pick up fine textured materials, leaving behind coarse sands and gravels. When water enters an old channel, cut off from the main river, the flow rate

decreases, giving the finer particles time to settle. This process produces the typical textural gradient observed along a transect from the top of a bar into a depression (Figure 1). Water table depth also changes along this transect and together these parameters determine the moisture regime at a given location.

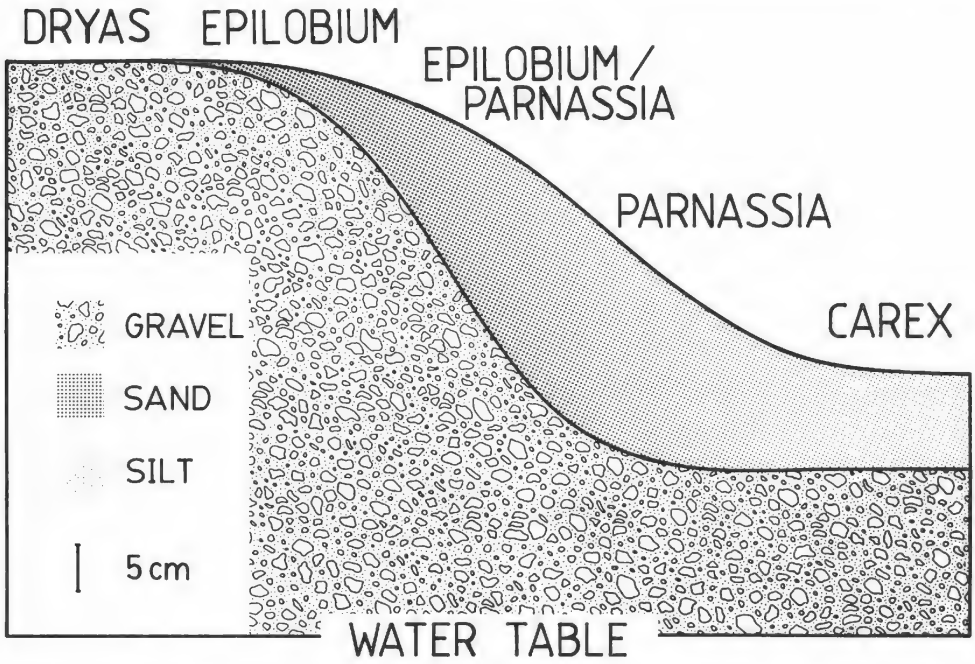

Figure 1. A schematic cross-section of the gravel bar showing the distribution of community types in relation to soil texture and water table depth.

Low moisture holding capacity and rapid drainage of the coarse gravel of the bar tops and the maximum observed water table depth in these locations makes them extremely dry during the growing season. Coarse textured soils have a low nutrient exchange capacity and, consequently are infertile (Black 1968). In addition, the compact nature of the gravel and preponderance of pebbles and stones make it difficult for establishing seedlings to develop a root system, reducing their ability to access what little moisture and nutrients are available.

In contrast, the silty soils of the depressional areas have a high moisture holding capacity and, while potentially well drained, are less permeable than the gravelly soils. The close proximity of the water table to the ground surface makes it more likely that plants can access capillary water, particularly since the silty material would not restrict root growth. The nutrient status of these sites would probably be better than the bar top locations because of the higher nutrient exchange capacity of fine textured soils. The main restriction to plant growth in silty depressions may be the frequency of flooding which causes the rooting zone to be saturated at regular intervals, particularly early in the growing season. This condition may lead to root oxygen deficiency with a concomitant reduction in root growth and nutrient uptake. In addition, wet soils warm up slowly in the spring so that onset of the growing season may be delayed (Brady 1974). Seedlings colonizing these sites would be completely submerged and subject to drowning during spring high water.

Depressional slope positions, while not as moist as the lower sites during the summer, would not be subject to prolonged submergence. Slope positions would have a more favorable

moisture regime than the gravel areas of the bar tops and therefore probably represent the most favorable environment for initial colonization of the bars.

Successional relationships among the community types may be inferred from patterns of floristic development (Mueller-Dombois and Ellenberg 1974). In the Blaeberry valley, plant succession on river terraces is directed toward a vegetation type dominated by *Populus trichocarpa* and *Picea glauca*. These two species are consistently found only in the Populus Stable Bar community type, suggesting that this community is successionally more advanced than others defined in this study.

The two phases observed within the Populus community indicate that this successional stage develops from both the Dryas Dry Gravel and Epilobium Shallow Sand community types. A well established *Dryas* mat will ameliorate the xeric, infertile conditions of the bar top by adding organic matter and nitrogen to the soil. During periods of flooding, the mat will reduce water velocity and act as a filter, increasing the deposition of silt which further increases moisture availability. With improved fertility and moisture conditions, less tolerant species can invade. Lawrence (1974) found that shrubs growing in old *Dryas* mats had higher growth rates than shrubs growing on bare glacial outwash. Citing the work of Cooper (1931), he suggested that *Dryas* was very shade intolerant and would quickly die out once other species had become established. Similar processes acting in the Epilobium community type would allow later successional species to invade in these areas.

Three releves of the Parnassia/Epilobium Deep Sand community type (22, 25, 26), may be successional predecessors of the Epilobium community type. In these releves the species of the Parnassia group are not abundant and are strongly dominated by *Epilobium latifolia*. The surficial sand layer in these sites is within the depth range of the Epilobium community. Local extinction of the Parnassia group species through competition with later successional species probably will occur in the future, producing stands that would be classified in the Epilobium community type.

Stands of the Populus community type were not found in depressions or in areas of deep sand or silt typical of the remaining releves of the Parnassia/Epilobium Deep Sand, Parnassia Silt Channel, and Carex Wet Depression types. These communities may be located in areas which remain too wet in the spring to permit the establishment of later successional species. They would be expected to become drier as river bed cutting lowered the water table but, since this is a slow process, it is likely that reactivation of the old channels by changes in river flow patterns would cause the destruction of these communities before succession could occur.

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Implications of Selenium Levels in Washington Mountain Goats, Mule Deer, and Rocky Mountain Elk

Abstract

Samples of mountain goat forage, hair, blood, liver, and fecal pellets were analyzed for selenium content. Wild mountain goats had selenium levels which rated as deficient when compared to selenium levels desirable for livestock. Captive goats, which consumed diets supplemented with 0.1 ppm selenium, had normal to high blood selenium levels compared to livestock. Selenium levels in liver and hair samples were higher for mule deer and elk than for wild mountain goats but the selenium levels in the liver samples ranked as deficient relative to livestock. Selenium deficiency is a cause of white muscle disease and has also been linked to reduced production and neonate survival. Selenium supplementation of wild ungulates is proposed in selenium deficient areas to increase herd health and production.

Introduction

Selenium has long been recognized as an essential element in livestock nutrition (Young *et al.* 1961, Muth and Allaway 1963, Oldfield *et al.* 1963, Jenkins and Hidiroglou 1972, Ammerman and Miller 1975, Andrews *et al.* 1976). Selenium deficiencies have been linked to white muscle disease (characterized by lesions of white striations and degeneration of muscle tissue), unthriftiness, weakness of newborn, reduced rate of weight gain, reduced production (because of increased infertility, stillbirths, and abortions), and a reduced immunosuppression system (Oldfield *et al.* 1963, Allaway and Hodgson 1964, Jenkins and Hidiroglou 1972, Ammerman and Miller 1975, Andrews *et al.* 1976).

Recently researchers have identified the importance of adequate selenium to wildlife (Hebert and Cowan 1971, Fleming *et al.* 1977, Lewis *et al.* 1977, Stoszek *et al.* 1980, Ullrey *et al.* 1981, Robbins 1983). Most of this wildlife research has been concerned with the influence of selenium on the occurrence of white muscle disease (Hebert and Cowan 1971, Fleming *et al. 1977, Ullrey et al.* 1981, Foster *et al.* 1983) and capture myopathy (acidosis and death caused by stress during capture and handling) (Chalmers and Barrett 1977, Lewis *et al.* 1977). Stoszek *et al.* (1980) and Ullrey *et al.* (1981) hypothesized that selenium deficiency was linked to lower reproductive rates for pronghorns (*Antilocarpa americana*) and white-tailed deer (*Odocoileus virginianus*), respectively.

Since the distribution of selenium in soils and plants varies greatly throughout the United States (Muth and Allaway 1963, Muth 1970, Ammerman and Miller 1975) it is likely that selenium concentrations also influence local wildlife populations. Selenium deficiency is recognized as a problem for livestock in the Northwest (Muth and Allaway 1963) and livestock growers now supplement their herds with selenium (P. South, personal communication). However, big game species that graze these same selenium deficient areas have not received the benefits of selenium supplementation.

Selenium deficiencies may be keeping big game herds from achieving their optimum productivity levels (Stoszek *et al.* 1980, Ullrey *et al.* 1981) Any influence of selenium deficiency on big game production would have been present for thousands of years. However, coupled with other limiting factors (e.g., reduction of winter ranges, human harassment, hunting mortality), selenium deficiency may be an additive factor which represses optimal herd growth.

Selenium concentrations in several big game species were studied as a part of wildlife studies required by the new Federal Energy Regulatory Commission license for the Lake Chelan hydroelectric project. The purpose of this study was to establish selenium concentration levels for mule deer (*Odocoileus hemionus*), mountain goats (*Oreamnos americanus*), and Rocky Mountain elk (*Cervus elaphus nelsoni*) and compare those levels with selenium levels found in livestock.

Methods

Mountain goat forage samples were collected along Lake Chelan in northcentral Washington for selenium analysis during the winters of

1982-83 and 1983-84. Feeding goats were backtracked and samples were taken from forage plants they had been eating. Samples of local forage species which have been identified in mountain goat food habits studies (Hjeljord 1973, Adams and Bailey 1983, Campbell and Johnson 1983, Fielder and McKay 1984) were also collected. The Washington State University (WSU) Washington Animal Disease Diagnostic Laboratory (WADDL) used the atomic absorption method to determine selenium content of the forage samples.

Selenium values were determined for mountain goats from fecal pellets, hair, blood, and liver samples. Fecal pellets were collected along Lake Chelan during winter forage collections, from goats immediately after they were trapped in Olympic National Park (ONP), and from goats in captivity at WSU and at the Woodland Park Zoo (WPZ) in Seattle.

Hair samples were taken from the hindquarters of mountain goats captured in ONP, goats in captivity at WSU and WPZ, and from goats harvested by hunters in the Cascade Mountains of Washington and mule deer and elk harvested in central Washington. Liver samples were also collected from the goats, mule deer, and elk harvested by hunters. The deer, mountain goat, and elk hair and liver samples were obtained on an "as available" basis. All of the deer sampled were harvested in Chelan County and the elk were harvested in Chelan and Kittitas counties. Blood samples were obtained from mountain goats captured in ONP and from captives at WSU and WPZ.

All of the samples (forage, fecal pellet, hair, liver, and blood) were sealed in plastic bags, kept as cool as possible until they could be frozen, and were kept frozen until analyzed. The samples were analyzed at WSU-WADDL by the atomic absorption method using a Perkin-Elmer 360 atomic absorption spectrometer with a MHS-10 mercury hydride system. Charles Robbins (WSU) also had 11 of those same blood samples from the ONP goats analyzed at Oregon State University by the fluorometric method (Whetter and Ullrey 1978), as part of his research and graciously shared those data.

Captive mountain goats at WSU were maintained on a selenium supplemented alfalfa-grain pellet (approximately 0.10 ppm Se), and received varying doses of selenium injections as part of a research project. The goats at WPZ utilize an apple-carrot-yam mixture which is supplemented with selenium (0.10 ppm), alfalfa hay (grown in eastern Washington), and Purina horse chow.

Results

All of the forage plants used by mountain goats along Lake Chelan during winter had either low or undetectable levels of selenium (Table 1). Hebert and Cowan (1971) found that mountain goat forages in southeast British Columbia were also low in selenium. A high proportion of the winter diet of the Lake Chelan goat herd is comprised of grasses and conifers (Fielder and McKay 1984) which included all with the highest selenium concentrations (Table 1).

TABLE 1. Selenium content (ppm) of mountain goat forage plants along Lake Chelan, Washington.

Forage plant	Shore	
	South	North
Bluebunch wheatgrass (*Agropyron spicatum*)	0	.02
Fescue spp. (*Festuca* spp.)	0	—
Bluegrass spp. (*Poa* spp.)	0	—
Needlegrass spp. (*Stipa* spp.)	.01	—
Paintbrush spp. (*Castillega* spp.)	—	0
Fumariaceae	0	—
Lewisia (*Lewisia columbiana*)	0	—
Penstemon spp. (*Penstemon* spp.)	0	0
Eriogonum spp. (*Eriogonum* spp.)	0	—
Unknown green forb	0	—
Unknown forb	—	0
Serviceberry (*Amelanchier alnifolia*)	0	—
Kinnikinnick (*Arctostaphylos uva-ursi*)	0	—
Red-osier dogwood (*Cornus stolonifera*)	TR	—
Oregon boxwood (*Pachystima myrinites*)	0	—
Antelope bitterbrush (*Purshia tridentata*)	—	0
Ponderosa pine (*Pinus ponderosa*)	TR	.03
Douglas fir (*Pseudotsuga menziesii*)	.02	.02
Sword Fern (*Polystichum munitum*)	0	0

TR = trace, — = no sample tested, 0 = none detected (detection of selenium concentrations less than .005 ppm was unreliable).

There is significant variation in selenium values of blood ($P < 0.01$), hair ($P < 0.01$), liver ($P < 0.01$), and fecal pellet ($0.01 < P < 0.05$) samples from the groups of mountain goats in Washington which we sampled (Table 2). Eleven

TABLE 2. Selenium concentrations (ppm) in several sample types from Washington mountain goats, Mule deer, and Rocky Mountain elk.

Sample group[1]	Sample size	Range	Mean	Standard deviation
Hair				
Washington St. Univ. goats	4	.12-.188	.148	.028
Woodland Park Zoo goats	7	.01-.047	.020	.013
Olympic National Park goats	22	.00-.087	.020	.023
Washington hunter kill goats	6	.04-.094	.070	.021
Washington hunter kill deer	10	.01-.314	.150	.080
Washington hunter kill elk	8	.05-.240	.110	.062
Blood				
Washington St. Univ. goats	3	.05-.21	.142	.086
Woodland Park Zoo goats	7	.20-.25	.222	.020
Olympic National Park goats	20	.01-.11	.035	.025
Olympic National Park goats[2]	11	.01-.15	.057	.056
Pellets				
Washington St. Univ. goats	4	.09-.21	.159	.057
Woodland Park Zoo goats	6	.02-.04	.029	.010
Olympic National Park goats	16	.00-.04	.009	.008
Lake Chelan goats	12	.01-.05	.020	.010
Liver				
Washington hunter kill goats	10	.01-.07	.022	.020
Washington hunter kill deer	10	.05-.20	.121	.057
Washington hunter kill elk	9	.02-.21	.070	.066

[1]All samples analyzed by atomic absorption method unless indicated.
[2]Samples analyzed by fluorometric method. These 11 samples were also among the 20 blood samples from ONP goats which were sampled by the atomic absorption method.

blood samples from ONP goats were analyzed by both the atomic absorption and fluorometric methods. The fluorometric method yielded selenium values for these samples which were slightly higher than those yielded by the atomic absorption method ($0.01 < P < 0.05$). Selenium concentrations in hair and liver samples from hunter harvested goats did not differ significantly from similar samples from deer and elk ($P > 0.05$). However, deer and elk hair and liver selenium levels ranged to as much as three times the concentration levels as samples from goats harvested by hunters (Table 2). The goats at WSU and WPZ had higher blood and fecal pellet selenium levels ($P < 0.01$) than did wild mountain goats.

Selenium concentrations in blood, liver, and hair samples from mountain goats, mule deer, and elk were compared to similar samples from domestic sheep, cattle, and hogs (Table 3). Selenium levels in the samples from goats at WSU (whose feed is supplemented with selenium) rate as normal or high compared to domestic livestock. Selenium levels in liver samples from elk and deer harvested by hunters rank as deficient compared to sheep and hogs. Wild mountain goats (those captured in ONP and those harvested by hunters) are deficient in selenium, compared to livestock (Table 3).

Discussion

Most mountain goat habitat in North America occurs in mountainous areas of volcanic origin with relatively new soils where selenium levels in forage would be expected to be relatively low. Mountain goat diets in Washington, like those in southeast British Columbia (Hebert and Cowan 1971), are low in selenium. Selenium levels were highest in conifers (Table 1), which comprise a major portion of the winter diet of mountain goats in Washington (Campbell and Johnson 1983, Fielder and McKay 1984). However, the

TABLE 3. A comparison of selenium levels in big game and livestock.

Animals/source	Average selenium levels or ranges (ppm)[1]		
	Blood	Liver	Hair
Big game			
Mule deer (hunters)		.12(.05-.20)	.15(.01-.31)
Rocky Mountain elk (hunters)		.07(.02-.21)	.06(.05-.24)
Mountain goats (hunters)		.02(.01-.07)	.05(.04-.09)
Mountain goats (WSU)	.14(.05-.21)		.15(.12-.19)
Mountain goats (WPZ)	.22(.20-.25)		.02(.01-.05)
Mountain goats (ONP)	.04(.01-.15)		.02(.00-.09)
Sheep			
Andrews *et al.* 1976	def. .010	def. .020	def. .050
Thompson *et al.* 1976	def. (.021-.067)		
Thompson *et al.* 1976	high (.133-.249)		
Jenkins and Hidiroglou 1972		def. (.08-.19)	
Burton *et al.* 1962		low .345 ± .12	
Burton *et al.* 1962		norm. .906 ± .06	
Jenkins and Hidiroglou 1972		norm. (.92-2.54)	
Cattle			
P. South, pers. comm.	def. <.05		
Thompson *et al.* 1976	low (.009-.072)		
P. South, pers. comm.	marg. (.05-.09)		
P. South, pers. comm.	norm. >0.1		
Perry *et al.* 1976			high .390(.214-.564)
Hogs			
Thompson *et al.* 1976	high (.093-.193)		
Jenkins and Hidiroglou 1972		def. (.19-.31)	
Jenkins and Hidiroglou 1972		norm. 1.82	

[1]def. = deficient, marg. = marginal, norm. = normal.

selenium levels in conifers browsed by goats along Lake Chelan are well below the levels needed for protection against white muscle disease. White muscle disease in domestic livestock is rare where selenium concentrations in forage is greater than 0.1 ppm, occurs erratically at 0.1-0.05 ppm, and is common where selenium concentrations in forage are less than 0.05 ppm (Muth and Allaway 1963, Allaway and Hodgson 1964). Although these concentration levels are linked with the occurrence of white muscle disease, they may also suggest warning levels for other selenium related problems which inhibit herd health (e.g., unthriftiness, weakness of newborn, reduced rate of weight gain, reduced production, and a reduced immunosuppression system).

Robbins and Parish (personal communication) report that captive goats exhibit a more rapid growth in captivity than do goats in the wild, suggestive of nutritional difficulties of wild mountain goats. This suggests that goats, on diets that are adequately supplemented, experience greater growth rates than unsupplemented goats as well as maintain higher selenium levels. The mountainous habitat occupied by mountain goats, usually characterized by relatively new, selenium deficient soils, may be a reason why goats harvested by hunters had lower hair and liver selenium levels which did not range as high as those of deer and elk (Tables 2 and 3). Deer and elk usually occupy lower elevations with older soils which are generally richer in selenium (Muth and Allaway 1963, National Research Council 1976).

Selenium deficiency in mountain goats (Hebert and Cowan 1971, this study) may be a factor contributing to low mountain goat productivity. Low selenium levels may be suppressing mountain goat production, just as it suppresses livestock production (Oldfield *et al.* 1963, Jenkins

and Hidiroglou 1972, Ammerman and Miller 1975, Andrews *et al.* 1976) by causing increased infertility, still births, and abortions and/or reducing neonate survival by causing weakness of newborn, slow weight gain, or a reduced immunosuppression system. Although estimates of mountain goat production vary among areas (from 86 to 22 kids per 100 adult females (Rideout 1978)) production rates are generally lower for mountain goats than for deer and elk. Doe:fawn and cow:calf ratios for deer and elk in central Washington and other selenium deficient regions are low compared to western regions with adequate selenium levels (e.g., Colorado, Utah, Montana, Wyoming). Stoszek *et al.* (1980) analyzed tissues from livestock and Idaho and Montana pronghorns and suggest a relationship between selenium deficiency in pronghorns and the decline of eastern Idaho pronghorn herds. Based upon analysis of white tailed deer muscle tissues, Ullrey *et al.* (1981) believe that deer in regions with low plant selenium concentrations may have a lower reproductive efficiency and a high postnatal mortality rate. Low production rates of mountain goat herds may also be, in part, a result of selenium linked reproduction and neonate survival limitations.

More research is needed to test this hypothesis including either (1) selenium analysis of big game samples from herds in several regions and correlation of selenium data with production data for those herds, or (2) monitoring of changes in productivity and newborn survival in big game herds, for which records of production are available, which have been supplemented with selenium (mineral or protein blocks). Selenium supplementation has been found to be desirable and effective by the livestock industry (Jenkins and Hidiroglou 1972, Wharger *et al.* 1978). Big game herds may also benefit from supplementation.

Acknowledgments

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Pollination Ecology of an Alpine Fell-Field Community in the North Cascades

Abstract

A study of the pollination ecology of an alpine fell-field located in the Mount Baker area of Washington State was conducted during the summer of 1981. Pollination syndromes (strategies) of the dominant plants were anemophily, generalized entomophily, and specialized entomophily. Insect visitations to plant species were quantified and flowering phenology was determined. The most important pollinators were bumblebees, syrphid flies, and muscoid flies; of lesser importance were butterflies and primitive flies. Plants exhibiting specialized entomophily appeared to minimize competition by separation of flowering times. Many of the plants exhibiting generalized entomophily flowered synchronously, perhaps as an adaptation to attract large numbers of flies by the colorful array of yellow and white flowers.

Introduction

Pollination ecology is a rapidly growing subdiscipline of "old-fashioned" biology, recently expanding from a primarily descriptive to an experimental science. However, although there are a number of excellent texts, e.g., Faegri and Vander Pijl (1979), Jones and Little (1983), Proctor and Yeo (1973), and Richards (1978), and numerous articles concerning pollination biology, there are few studies that deal specifically with pollination ecology of alpine communities. This is especially true of the North Cascades.

The most commonly cited insect pollinator groups (orders/families) in alpine areas of North America are bumblebees (Hymenoptera/Apidae); syrphid flies (Diptera/Syrphidae); Muscoid flies (Diptera/Anthomyidae, Muscidae, Calliphoridae, Sarcophagidae, Tachinidae); and butterflies (Lepidoptera/Papilionoidea, Lycaenidae, Satyridae, Nymphalidae) (Moldenke 1976, 1979; Moldenke and Lincoln 1979; Levesque and Burger 1982; Bauer, 1983).

Bumblebees are social insects and must forage for colony needs as well as their own. Accordingly they forage very intensively and visit numerous flowers. As a whole, the colony assumes a generalist role, visiting a wide variety of flower types. However, individuals tend to specialize (major) on one or two species at any given time (Heinrich 1976a, 1979). Many plant species are more-or-less dependent on bumblebees for pollination and have developed sequential flowering times (Pojar 1974; Reader 1975; Heinrich 1975, 1976b; Pleasants 1980; Bauer 1983), reducing competition for pollinators. Foraging behavior of flies and butterflies is variable and less well known (Proctor and Yeo 1973, Faegri and Vander Pijl 1979). In general, flies prefer flowers with non-concealed rewards, do not specialize, and appear in alpine communities early in the season. Butterflies prefer tubular flowers with concealed rewards, have a higher level of floral constancy than flies, and appear much later in the season.

For our study an alpine plant community was selected because of its simplicity, lack of disturbance, and, perhaps, more obvious plant-insect coadaptations, i.e., relationship between floral morphology/color and type of insect pollinator. By definition (Douglas and Bliss 1977) the alpine is that area in the mountains above the limit of upright tree growth, characterized by soil and weather extremes (Bliss 1971, Billings 1974). Our study consisted of analyses of flowering phenology and insect visitation. Flowering phenology is an important component of pollination ecology because it determines the availability of resources to animal pollinators and the competitive relationships among plants for these pollinators (Levin and Anderson 1970, Mosquin 1971, Pojar 1974, Heinrich 1975, Proctor 1978, Pleasants 1980). The pattern of pollinator visitation is important because it has a direct effect on the reproductive success and gene flow rate of plants (Macior 1971, Proctor and Yeo 1973, Richards 1978, Faegri and Vander Pijl 1979), and makes it possible to quantitatively assess the importance of specific pollinators within an alpine (in this case) community.

Methods

The selected study site was an alpine fell-field located near Mt. Baker on Chowder Ridge, a proposed research natural area (Tayor and Douglas 1978) (Figure 1). The ridge is relatively inaccessible and remains undisturbed. The area of sampling consisted of a 20 x 20 m plot on a moderate SE slope at ca. 2041 m elevation. The rocky ridgetop was sparsely vegetated by clumped, cushion plants, a typical fell-field community (Taylor and Douglas 1978). The community structure was determined in August 1980, using the experimental design described by Bliss (1963). In total, sixty 20 x 50 cm quadrats were used for measuring coverage (following Daubenmire 1959, 1968) and frequency. Importance or prominence values were calculated for each plant species by multiplying its mean percent cover by the square root of its frequency. Plants were identified using Hitchcock and Cronquist (1973) and Hitchcock *et al.* (1955-1969).

The pollination study was carried out during the summer of 1981. Plant species of the fell-field community were assigned a floral color class, following the system described by Kevin (1972a). The color class assignment does not relate to the insect visual range, which at least in some cases extends into the ultra-violet spectrum. Following Proctor and Yeo (1973), floral morphology was classified into the following types: (1) open—more-or-less bowl-shaped with exposed rewards; (2) partially exposed—usually some portion of the perianth fused resulting in somewhat difficult access to rewards; (3) closed—flower structured in such a way so as to exclude visitation by non-specialized pollinators; (4) small tubular—flowers with short tubular corollas, e.g., compositae, with little restriction of rewards; (5) large tubular—long tubular flowers requiring long "tongued" insects to reach concealed nectar. On the basis of floral morphology, plant species were assigned pollination strategies: wind (anemophily), generalist (generalized entomophily), specialist (specialized entomophily). See Table 1 for pollination strategies and related characteristics of the predominant plant species of our study.

Within the 20 x 20 m study area, insect group activity was quantified using 20 m transects (randomly selected from meter loci 1 through 20) and 2 m square observation plots (randomly selected from the 100 possible). All insect visits to flower species, including each of multiple visits by single insects, were recorded both while walking slowly along the transects and during 20 minute watch periods of the 2 m square plots. The number of watch periods and transects were limited by time to a maximum of six per day. In addition to the quantitative data collected from the study area, pollinator behavior was noted along the full length of Chowder Ridge periodically during the summers of 1980-1984.

An attempt was made to collect representatives of each discernable flower-visiting insect for identification to genus or family. Identifications were made using Borrer *et al.* (1976) and were confirmed by G. Kraft (Western Washington University).

An analysis of four bumblebees and eight syrphid fly pollen loads was made to supplement constancy determinations based on observed insect behavior. For bumblebees, corbiculae were used; for syrphid flies the entire insect was used, thus counts included pollen within the gut as well as grains attached externally. Percent pollen types was determined for each insect.

Flowering phenology was quantified using four 20 m permanent transects. The location of the transects was established by marking the northern and southern borders of the study area at 1 meter intervals (1-20) and randomly choosing a meter locus (1-4, 6-9, 11-14, 16-19) from within each of the four 5-meter intervals. All open flowers (flower clusters in the case of dense inflorescences, e.g., those of *Oxytropis campestris, Phacelia sericea, Solidago multiradiata,* and *Sedum lanceolatum*) within a one meter swath along the transect were counted. Phenology was recorded once each week throughout the 1981 flowering season.

Results and Discussion

The plant species of the Chowder Ridge fell-field community are listed in Table 1, along with their prominence value (PV), pollination strategy, floral morphology, floral color, and insect visitors. Dominant plants, based on PVs, were *Oxytropis campestris, Cerastium arvense, Agropyron caninum, Phlox diffusa,* and *Potentilla diversifolia.* Bare ground exceeded 50 percent coverage (69 percent), a characteristic of fell-field communities (Douglas and Bliss 1977). Plants were scattered, typically clumped, and most exhibited a cushion growth form.

Among the principal plant species, the "open" floral morphology was most common, followed in order of decreasing occurrence by "inconspicuous" (graminoids), "small tubular" (compositae), "partially exposed," "large tubular," and "closed." The latter two types were each represented by a single abundant species. Predominant floral colors were yellow and white.

Flower Visitors

Table 2 presents numbers of insect visits to flowers or inflorescences of principal plant species, as determined by watch periods and transects. Unfortunately, based on supplementary observations, the numbers are biased. During visits to Chowder Ridge prior to July 28, inclement weather (fog, rain, and even snow) restricted insect activity, especially that of bumblebees, butterflies, and syrphid flies. Thus, early flowering species typically pollinated by these insects, e.g., *Phlox diffusa, Silene acaulis, Phacelia sericea, Oxytropis campestris,* and *Potentilla* species, have lower visitation numbers than would be expected. Also, in *Phacelia sericea, Sedum lanceolatum,* and the Compositae, the entire inflorescence was treated as a single unit resulting in comparatively low visitation numbers since insects tended to probe several flowers per inflorescence for each recorded visit.

Major flower-visiting insects, discussed below, were bumblebees, syrphid flies, muscoid flies, butterflies, and primitive flies. Although primitive flies are not generally thought to be important alpine pollinators, Levesque and Burger (1982) listed dance flies (Empididae) among visitors to *Minuartia groenlandica* and Kevan (1972b) considers empids to be important pollinators in the high arctic.

Bumblebees—Three bumblebee species were observed visiting flowers within the study community on Chowder Ridge: *Bombus melanopygus, B. flavifrons,* and *B. boleatus,* the latter observed infrequently. These bees preferred the "insect specialist" flowers of *Oxytropis campestris* and *Phacelia sericea* when available early in the season, *Sedum lanceolatum, Solidago multiradiata,* in midseason, and *Aster sibiricus* in late season (see Table 2). The latter three species have "generalist" pollination strategies. Other "generalists" were visited by bumblebees but probably only exploratorily since so few visitations were recorded. Finally, bumblebees were unavailable to take advantage of the early-flowering and very abundant *Phlox diffusa* during the 1981 season (See Table 2). However, we have frequently observed queen bumblebees foraging on *Phlox diffusa* on Chowder Ridge.

Pollen types collected from four bumblebees suggest that those bees were majoring on two species at one time (see Table 3).

Syrphid flies—Syrphids, represented by several species, did not become abundant in 1981 until late July. After this time they were frequent visitors to most generalist plants and were observed to visit species with other pollinations strategies, including graminoids (*Carex phaeocephala* and *Poa alpina*) and *Phacelia sericea.* In these cases, the syrphids probably foraged on pollen without contacting stigmas and without effecting pollination.

Pollen samples from eight syrphid flies indicated variable foraging behavior. Some insects fed exclusively on one plant species while others exhibited little constancy (see Table 3). Syrphids had large visitation numbers, as shown in Table 2, suggesting their importance as pollinators in alpine habitats. They preferentially foraged on cushion plants with dense mats of flowers, e.g., *Saxifraga bronchialis* and *Cerastium arvense,* with several flowers typically being sampled from each plant.

Muscoid flies—Muscoid flies were represented by numerous species of four families: Anthomyidae, Muscidae, Callophoridae, and Tachinidae, the anthomyids being the most abundant. The muscoids were present in the fell-field community throughout the season and, along with primitive flies, were abundant early in July when other pollinators were unavailable or were inactivated by the cold and inclement weather. Like the syrphids, these flies preferred open, bowl-shaped flowers such as those of *Cerastium arvense, Saxifraga bronchialis,* and *Potentilla* spp., and had high visitation numbers (see Table 2). They also visited the short-tubular flowers of various Compositae.

Butterflies—Several species of butterflies (lepidopterids) were observed in the fell-field community, the most abundant being checkerspots and tortoise shells (*Nymphalidae*) and blues (*Lycaenidae*). Other lepidopterids observed were anglewings and fritillaries (*Nymphalidae*), whites

TABLE 1. Prominence values (PVs) and pollination related characteristics[a] of plants in the fell-field community on Chowder Ridge.

Plant Species	PV	Pollination Strategy	Floral Morphology	Floral Color	Insect Visitors[b]	
					Major	Minor
Oxytropis campestris	80	Insect-spec	Closed	Yellow	Bu	—
Cerastium arvense	72	Insect-gen	Open	White	Sf,Mf	Bu,Bf,Pf
Agrophyron caninum	60	Wind	Inconspicuous	Not/appl	—	—
Phlox diffusa	57	Insect-spec	Large-tubular	Pink	Bu,Bf	Sf,Mf
Potentilla diversifolia	46	Insect-gen	Open	Yellow	Sf,Mf,Pf	Bu,Bf
Sedum lanceolatum	29	Insect-gen	Open	Yellow	Bu,Bf,Sf,Mf	—
Saxifraga bronchialis	26	Insect-gen	Open	White	Sf,Mf	Pf,Bf
Phacelia sericea	22	Insect-spec	Part. exposed	Purple	Bu,Sf	Mf
Poa alpina	16	Wind	Inconspicuous	Not/appl	—	Sf
Achillea millefolium	10	Insect-gen	Short-tubular	White	Mf	Sf,Bf
Potentilla Villosa	07	Insect-gen	Open	Yellow	Sf,Mf,Pf	Bu,Bf
Solidago multiradiata	05	Insect-gen	Short-tubular	Yellow	Bu,Bf,Sf	Mf
Haplopappus lyallii	02	Insect-gen	Short-tubular	Yellow	Bu,Bf	Sf
Festuca ovina	02	Wind	Inconspicuous	Not/appl	—	—

Table 1 (continued)

Plant Species	PV	Pollination Strategy	Floral Morphology	Floral Color	Insect Visitors[b]	
					Major	Minor
Aster sibiricus	01	Insect-gen	Short-tubular	Purple	Bu,Bf	Mf
Carex albonigra	01	Wind	Inconspicuous	Not/appl	—	—
Carex phaeocephala	01	Wind	Inconspicuous	Not/appl	—	—
Erigeron compositus	01	Insect-gen	Short-tubular	White	Bf,Mf	Sf,Pf
Silene acaulis	01	Insect-spec	Part. exposed	Red	Bf,Bu	—
Anemone multifida	<01	Insect-gen	Open	White	—	—
Antennaria alpina	<01	Insect-gen	Short-tubular	White	—	—
Campanula rotundifolia	<01	Insect-spec	Large-tubular	Blue	Bu	Sf
Draba lonchocarpa	<01	Insect-gen	Part. exposed	White	—	—
Draba paysonii	<01	Apomixis	Part. exposed	Yellow	—	Pf
Sibbaldia procumbens	<01	Insect-gen	Open	Yellow	—	—
Trisetum spicatum	<01	Wind	Inconspicuous	Not/appl	—	—

[a]See the methods section for a full description of pollination related characteristics.

[b]Determination of major (primary) and minor (secondary) insect visitors is based on general observations as well as quantitative data given in Table 2.

Bu = bumblebees, Bf = butterflies, Sf = syrphid flies, Mf = muscoid flies, Pf = primitive flies.

TABLE 2. Number of observed insect visits to flowers or inflorescences during 2 meter plot watch periods/transects walks.[a]

Plant Species[b]	Insect Visitors				
	Primitive Flies	Syrphid Flies	Muscoid Flies	Butterflies	Bumblebees
Aster sibiricus	—	—	—	1/0	19/0
Achillea millefolium	—	0/1	—	—	—
Cerastium arvense	10/5	134/18	63/22	—	1/0
Erigeron compositus	2/1	9/3	7/1	7/0	—
Oxytropis campestris	—	—	—	—	33/10
Phacelia sericea	—	56/21	3/1	—	61/28
Phlox diffusa	—	3/1	1/0	—	—
Potentilla diversifolia	7/13	7/11	7/15	—	0/1
Potentilla Villosa	1/0	28/10	43/12	—	—
Saxifraga bronchialis	—	224/21	105/14	0/1	—
Sedum lanceolatum	—	67/16	6/1	6/1	245/18
Solidago multiradiata	—	81/4	22/1	2/0	9/0
Total	20/19	609/106	257/67	18/2	368/57

[a]The number of visitations to *Achillea* and *Phlox* are lower than expected because peak flowering for *Achillea* was after counts were made and *Phlox* flowered before its major pollinators appeared in the fell-field.

[b]Some species of the fell-field community were not observed to be visited by insects during watch periods or transects and are therefore not included here.

(*Pieridae*), skippers (*Hesperiidae*), swallowtails (*Papilionidae*), alpines (*Satyridae*), and several undetermined moths. The lepidopterids primarily visit tubular flowers such *Phlox diffusa, Silene acaulis* and Compositae, utilizing their long probing/sucking mouth parts to reach concealed nectar. In 1981, however, butterflies were not observed on Chowder Ridge until after 6 August, when *Phlox* and *Silene* had finished flowering (see Figure 3 and Table 2). In subsequent years we have observed butterflies foraging on these cushion plants on Chowder Ridge.

Primitive flies—These flies were represented by three families: Mycelophilidae (fungus gnats), Bibionidae (March flies), and Empididae (dance flies). They were abundant early in the flowering season and were most frequently observed on *Potentella diversifolia, P. villosa,* and *Cerastium arvense.*

Miscellaneous insects—Other observed flower visitors included ladybird beetles (Coleoptera/Coccinelidae), plant bugs (Hemiptera/Miridae), and solitary bees (Hymenoptera/family undetermined). These insects were not considered to be important pollinators. The bugs and beetles did not fly from flower to flower and lacked pollen carrying capacity, and solitary bees were rare in the community (three individuals observed during two field seasons). However, ladybird beetles were common and were frequently observed with their heads buried in flowers, apparently seeking nectar.

Pollination Strategies

Three pollination strategies were well represented among the dominant plant species of the fell-field community: wind (*Agropyron caninum* and *Poa alpina*), insect generalist (*Cerastium arvense* and *Potentilla diversifolia*), and insect specialist (*Oxytropis campestris* and *Phlox diffusa*). See Table 1 for a summation of pollination strategies and prominence values. One of the conspicuous species of the fell-field community, *Draba paysonii,* is reportedly agamospermic (Mulligan 1971). This dense cushion plant was the first to flower in the fell-field community and was visited only by primitive flies.

Flowering Phenology and Pollination Patterns

Figures 2-4 depict the flowering periods of twelve common insect pollinated plants in the fell-field community during 1981. The first of these plants to peak in flowering was *Phlox diffusa.* This

TABLE 3. Pollen types, as percentages of total pollen load, from corbiculae of *Bombus melanopygus* and from whole body analyses of syrphid flies.

Insect	Date Captured	Host Plant	Pollen Types								
			Phacelia	Oxytropis	Sedum	Phlox	Cerastium	Compositae	Potentilla	Saxifraga	Undetermined
Bombus 1	8/2	Oxytropis	60	39							1
Bombus 2	8/2	Phacelia	32	63							5
Bombus 3	8/12	Sedum		46	42			5			6
Bombus 4	8/14	Sedum		13	80			7			
Syrphid 1	8/12	Phacelia	19			19		60			2
Syrphid 2	8/12	Saxifraga	2				1	1		96	
Syrphid 3	8/12	Potentilla					32	4	64		
Syrphid 4	8/13	Compositae	4				4	58		33	1
Syrphid 5	8/13	Saxifraga	1				29	16		54	
Syrphid 6	8/13	Saxifraga	26				2	33		38	1
Syrphid 7	8/13	Saxifraga					45	10		36	9
Syrphid 8	8/14	Saxifraga	31				8		29	35	6

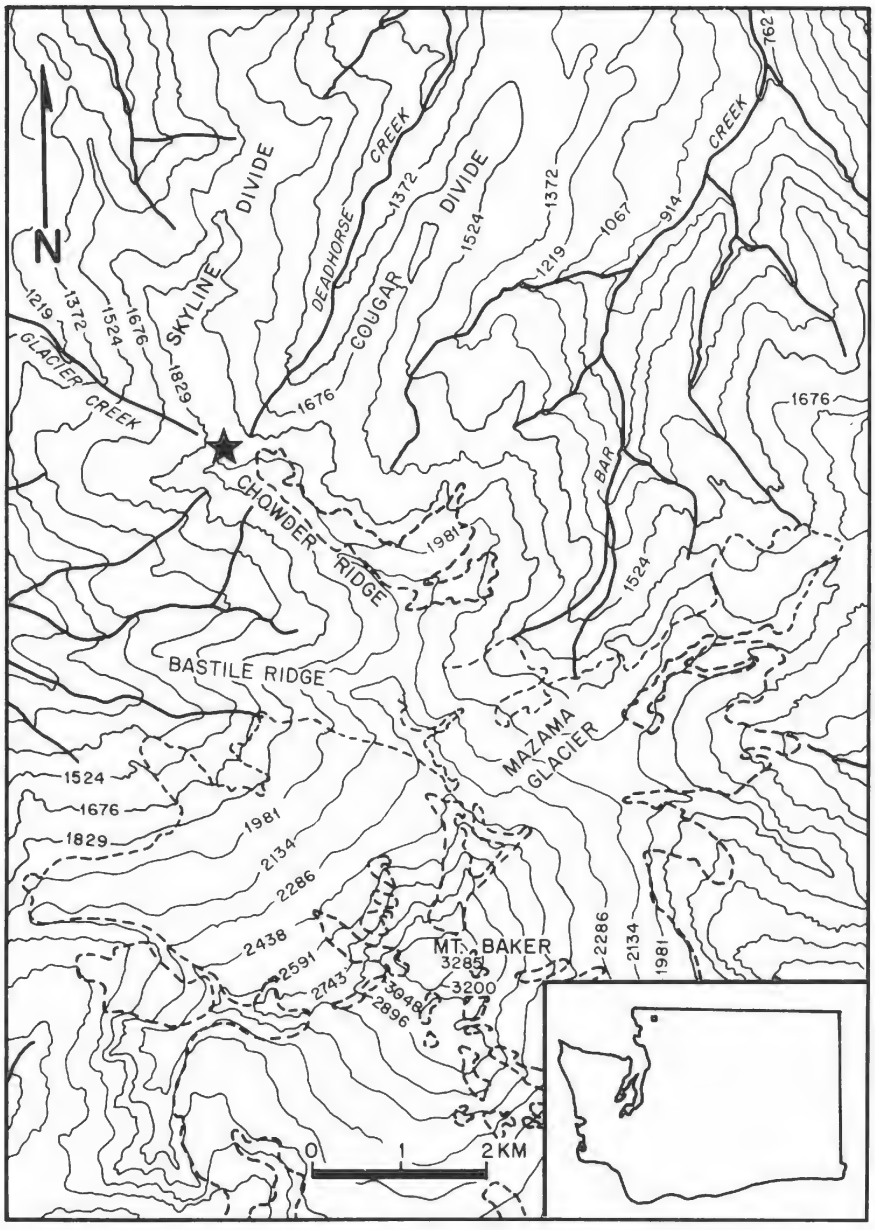
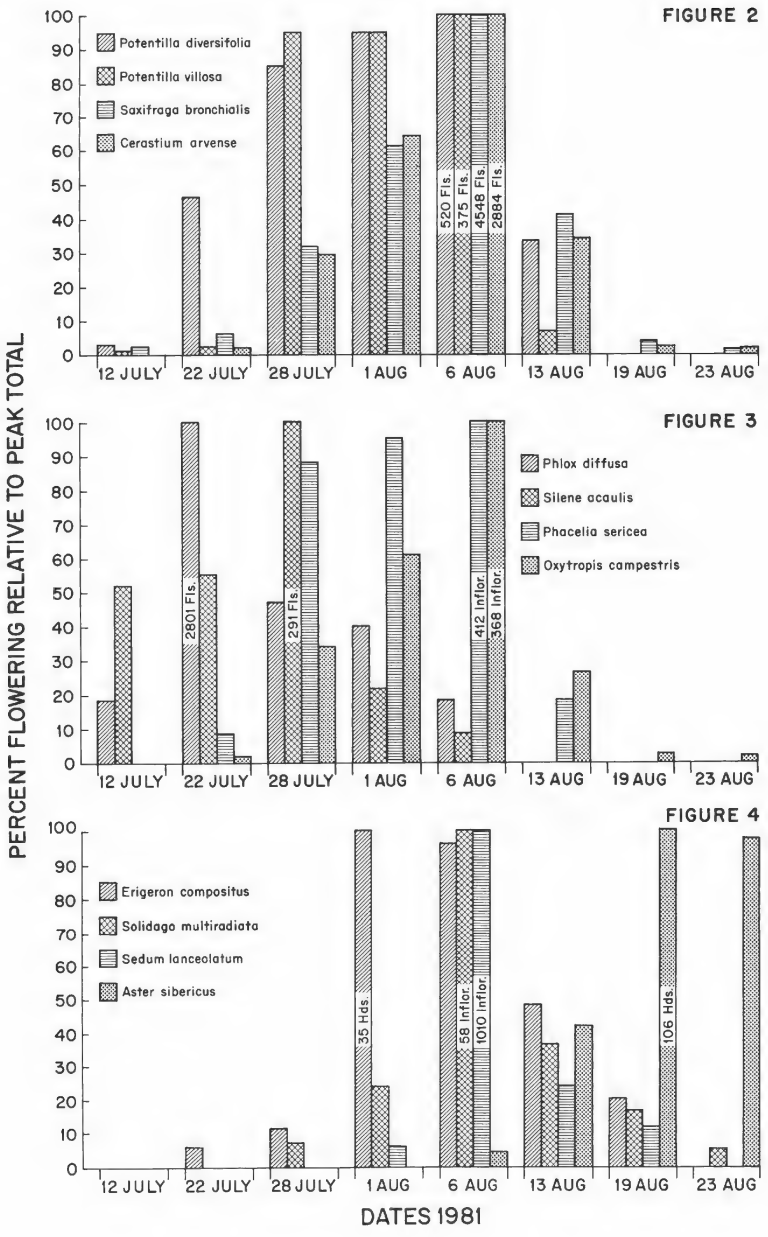


Figure 1. Map showing the location of the study area (star): Chowder Ridge, Mount Baker area, Whatcom County, Washington.



Figures 2-4. Flowering periods of major entomophilous species in the alipine fell-field.
Figure 2: Insect generalist flowers with open floral morphology.
Figure 3: Insect specialist flowers: partially exposed (*Phacelia* and *Silene*), large tubular (*Phlox*), and closed (*Oxytropis*) floral morphology.
Figure 4: Insect generalist flowers: short tubular (compositae) and open (*Sedum*) floral morphology.

early flowering trait seemed non-adaptive since the specialist pollinators were not yet available at this time (see Table 2 and Figure 3). However, in years subsequent to 1981, butterflies and, especially, bumblebees have been observed visiting *Phlox. Phlox* is most likely an important nectar source for early season queen bumblebees.

Potentilla villosa and *P. diversifolia* flowered synchronously as did *Cerastium arvense* and *Saxifraga bronchialis* (see Figure 2). These four insect generalists had a recorded (1981) peak flowering time of 6 August. This seems at odds with the popular theory that the flowering phenologies of species sharing pollinators tend to diverge, increasing pollination efficiency and reproductive success (Levin and Anderson 1970, Mosquin 1971). However, synchronous flowering may serve to attract greater numbers of potential pollinators to alpine communities, mostly flies in this case, increasing the chance of cross pollination. Macior (1971) suggested this as a possibility in the alpine where topography and climate often limit plant population size. This idea is supported by Williams and Batzli (1982) who showed increased seed set in interspecific stands of *Pedicularis* as opposed to single species stands. A third interpretation is that synchronous flowering is simply a reflection of genetically based opportunism, i.e., of the plants' ability to take advantage of a limited suitable flowering period, and has little to do with coadaptation with insects or with interspecific interaction.

In contrast to those of fly-pollinated plants, peak flowering times of bumblebee majors were spread over several weeks (see Figures 3 and 4). In this respect, the Chowder Ridge fell-field is similar to other communities where bumblebees are important pollinators (Reader 1975, Heinrich 1976b, Pleasants 1980). Again, however, caution should be taken in interpreting these results. The apparent competitive displacement of flowering times as exhibited by bumblebee majors, especially those with generalist pollination strategies, may also simply reflect opportunism, this time on the part of the bees. Since bee colonies depend on a continuous source of floral foods, they necessarily major on species with temporally dispersed phenologies. Species such as *Aster sibiricus* then become bee majors *because* they are available at an opportune time, rather than having evolved separate peak flowering periods in response to competitions for bumblebee pollinators.

Phenological data have not been provided for: *Achillea millefolium,* which achieved peak flowering after 1 September, the date that field analyses were terminated; *Haplopappus lyallii,* which by chance did not occur along the phenology transects; and plants with prominence values of less than 01 (see Table 1).

Conclusions

Although we cannot quantify the relative importance of pollinators in the Chowder Ridge fell-field community, it is obvious from numbers of flower visitations that bumblebees, syrphid flies, and muscoid flies are all very important, butterflies and primitive flies less so. The relationship between floral morphology and insect visitor was consistent with expectations based on publications cited herein. The results of phenological analyses indicate that plants with generalist pollination strategies tend to flower synchronously, perhaps as an adaptation for greater insect attraction, while those with specialist strategies flower sequentially, perhaps due to competitive displacement. It is suggested, however, that these results may merely reflect opportunism on the part of the plants and specialist pollinators (bees) respectively. Finally, observations of alpine communities on Chowder Ridge over a several year period have resulted in our appreciation of the year to year variation in flowering phenology. The flowering sequence of representative species remains more or less consistent but the time of the flowering peak, the length of the flowering period, and the extent of flowering overlap vary considerably according to vagaries of the weather. Also, the availability of "preferred" pollinators is influenced by the weather, a case in point being the apparent absence of butterflies and bumblebees during the peak flowering period of *Phlox diffusa* in 1981. The alpine communities of Chowder Ridge are especially sensitive to climatic fluctuations because of the south-facing exposure and associated water stress.

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Reproductive Colorations, Paternal Behavior and Egg Masses of Kelp Greenling, *Hexagrammos decagrammus*, and Whitespotted Greenling, *H. stelleri*

Abstract

Males and females of *Hexagrammos decagrammus*, a northeastern Pacific greenling with striking sexual differences in fundamental color patterns, exhibit different sexual dichromatisms during courtship. Males of *H. decagrammus* and its congener, *H. stelleri*, defend benthic adhesive eggs against conspecifics and other fishes. Males often simultaneously tend > 1 mass of spawn; circumstantial evidence suggests that these eggs are the clutches of > 1 female.

Introduction

The kelp greenling, *Hexagrammos decagrammus*, inhabits shallow rock reefs from the Aleutians to southern California (Eschmeyer *et al.* 1983) and contributes significantly to shore, skiff and skindiving recreational fisheries, particularly in northern California (Frey 1971) and Puget Sound (Barker 1979). The whitespotted greenling, *H. stelleri*, a smaller and less exploited species, inhabits coastal rocky and vegetated regions (Hart 1973) from Puget Sound to northern Japan (Eschmeyer *et al.* 1983).

Little has been published on the reproductive biology of either species to complement Kendall and Vinter's (1984) recent review of the larvae of these and other hexagrammids. *Hexagrammos decagrammus* spawns masses of blue eggs during the fall in British Columbia (Hart 1973) and Puget Sound (Patten 1980), and during late summer farther north (Gorbunova 1970). Feder *et al.* (1974) inferred winter spawning in southern California, because of springtime observations of planktonic larvae and benthic juvenile recruits. *Hexagrammos stelleri* also spawns clusters of blue eggs (Hart 1973) during late summer-winter, depending on latitude (Gorbunova 1970, Hart 1973, Barker 1979, Patten 1980). In this paper I provide new information on spawned eggs and clutches, spawning substrates, and reproductive colorations and paternal behaviors of these two hexagrammids.

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Study Areas and Methods

Most observations of *Hexagrammos decagrammus* were made during October-December 1972 and November 1973 at natural and artificial rock reefs in Puget Sound and adjacent waterways and during December 1973 and December 1974-January 1975 at natural reefs off Cannery Row, Monterey, California. The physical characteristics and biotas of these areas are described by DeMartini and Anderson (1980). Additional observations were made off Mitchell, Eagle and Limestone Points on San Juan Island, Washington (48° 30' N, 123° 05' W) during October-December 1972. Underwater observations were made using SCUBA at depths of 0-15 m (Washington) and 5-10 m below MLLW (Monterey). Incidental observations were made at 9-25 m depths on a submerged seamount off Point Buchon (35° 15' N, 120° 54' W) in central California during December 1976. Some low intertidal spawns in Puget Sound were surveyed while emergent during nighttime minus tides.

Observations of *H. stelleri* were made during October 1972 in the cove immediately offshore of the Friday Harbor Laboratories (FHL) of the University of Washington on San Jan Island, Washington (see Shimek, 1983, for habitat description). Observations of *H. stelleri* were made in and near an eelgrass (*Zostera marina*) bed at depths of 3-16 m.

SCUBA observations were made during 0930-1630 h (PST) when lateral underwater visibilities exceeded 3 m. Notes were recorded on plastic slates and later transcribed to permanent records.

The Washington and Monterey observations I describe complement detailed field studies of the population ecology and mating system of another hexagrammid, *Oxylebius pictus* (DeMartini and Anderson 1980, DeMartini 1985).

Observations

Reproductive Colorations and Spawn Tending

Kelp greenling. On dives of 5 December 1974 and 1 January 1975 at Monterey, I observed two different male *Hexagrammos decagrammus,* both engaged in interactions with a gravid-appearing female. When first sighted at 1000-1300 h, the males and females were on the bottom, within .5-m distance of each other, on inclined surfaces of reef. One pair was adjacent to two masses of *H. decagrammus* spawn, both in early (unpigmented) developmental stages, that were nestled amongst encrusting epifauna. In both instances, the male mostly lacked the fundamental male color pattern illustrated by Eschmeyer *et al.* (1983: Plate 22); instead, each was uniform, dark slate-grey on its anterior, as well as posterior trunk. The typical pattern of blue, stellate spots (outlined in reddish-brown) was especially pronounced on the head region of the males. (Such "spawning" coloration has been noted previously by Hart, 1973, from aquarium observations.) The eyes of both males had a conspicuous, unusually bright golden sheen. Both females also lacked the fundamental pattern of uniform, small reddish-brown spots (Eschmeyer *et al.* 1983); trunk coloration of the females was dominated instead by numerous, large (several cm-wide) dark-brown blotches.

Male *H. decagrammus* were observed tending from one to six masses of spawn on seven other occasions off Monterey. Twenty-one male *H. decagrammus* were observed tending from one to ten (mean = 4.5) masses of spawn at reefs in Puget Sound and near San Juan Island, Washington. Spawns were found over the range of depths surveyed off Monterey and at depths from +1 to −14 m in Washington waters. Neighboring masses within male broods were adjacent to 1.9 m apart. Water temperatures were 9-12°C.

Hexagrammos decagrammus eggs were usually deposited among encrusting epifauna, often the empty valves of the large barnacle, *Balanus nubilus.* At Buchon Reef, one mass of spawn was sequestered between the branches of a colony of living hydrocoral, *Allopora californica,* at 15-m depth. A minority of all egg masses were laid directly on rock substrate.

All solitary male *H. decagrammus* observed tending spawn on reefs off Monterey and Washington had the usual male color pattern illustrated by Eschmeyer *et al.* (1983). On two occasions in Puget Sound, a male did not retreat when I approached with 1-2 m of the spawn it was tending, and maintained its fundamental sexual dichromatism.

Tending and nontending male *H. decagrammus* were seen chasing conspecific males on Puget Sound reefs. I once saw a nontending male chasing an adult copper rockfish, *Sebastes caurinus,* on a reef near San Juan Island during the breeding season. Males maintained their fundamental sexual dichromatism during intra- and interspecific chases.

Whitespotted greenling. The body and fin colorations of male *Hexagrammos stelleri* observed at the FHL cove differed from the typical color pattern illustrated by Eschmeyer *et al.* (1983: Plate 22). On dives of 14 October 1972 (1230-1400 h) and 22 October 1972 (1520-1630 h), I saw seven male *H. stelleri.* Individuals were recognized by differences in body size and location within the eelgrass bed. One male was noted attacking another male. Four fish circled me aggressively; and two males bit my facemask. One of the latter fish (ca. 30 cm total length, TL) chased a female *H. decagrammus.* This male was guarding seven masses of spawn at a depth of 8 m. Six masses had been laid among the branches of a red alga (*Aghardiella* sp.), and the other was nestled in the holdfast of a laminarian kelp, < 10-cm distant. Another fish (a mature male 25 cm TL, collected by spear and sex confirmed by dissection) was guarding three masses of spawn at 7 m. All eggs had been spawned in branches of the red alga *Prionitis* sp. Both guardian fish had unusually dark bodies, noticeably dusky pelvic and anal fins, and each had a conspicuous black blotch on the anterior dorsal fin. The sexually monomorphic white spotting characteristic of the species (Rutenberg 1970, Eschmeyer *et al.* 1983) was present on the body and head of both males. Water temperature was 10°C.

Spawn Characteristics

Kelp greenling. Thirty-two discrete golf ball- to tennis ball-sized masses of benthic adhesive eggs were collected from substrates near paternal male *Hexagrammos decagrammus* at reefs in Puget Sound and near San Juan Island, Washington. The number of eggs present in each mass was determined by wet gravimetric method (Bagenal and Braum 1971) to the nearest mg. Egg number varied from 1,580-9,660 (mean = 4,340; SD = 1,760) for these 32 spawns. Eggs (including capsules) ranged from 2.2-2.5 mm (mean = 2.3 mm) in diameter and 6.8-8.7 mg (mean = 7.6 mg) live weight. Each mass of *H. decagrammus* spawn tended by an individual male usually differed in yolk coloration (from rose, green, and blue, to grey) and developmental stage. Fertilized eggs contained numerous, small whitish to yellow-orange oil globules. Older masses of spawn often had a luxuriant diatom epiflora. Embryos required about 30 days to progress from pre-germ ring stages to hatching when held in the laboratory at 10°C.

Whitespotted greenling. The ten masses of *Hexagrammos stelleri* spawn contained from 1,200-5,200 embryos each (mean = 3,460; SD = 1,060). Eggs ranged from 2.0-2.5 mm (mean = 2.2 mm) in diameter and 5.2-7.1 mg (mean = 6.4 mg) live weight. Egg masses differed in yolk coloration (ranging from green, blue, and violet, to grey) and stage of embryonic development. The numerous, small oil globules ranged from pale straw to golden in color. Embryos required about 30 days to hatch at 10°C.

Discussion

Territorial Spawn Tending and Reproductive Colorations

Male *Hexagrammos decagrammus* are both inter- and intraspecifically territorial (Barker 1979, this study). Male defense of spawn and spawning sites has been described for several other eastern Pacific greenlings (lingcod, *Ophiodon elongatus:* Lariviere *et al.* 1981 and references; painted greenling, *Oxylebius pictus:* DeMartini and Anderson 1980, DeMartini 1985) and is suspected for hexagrammids in general (Gorbunova 1970).

The courtship colorations of male and female *H. decagrammus* are sexually distinct variations of the species' fundamental sexual dichromatism. *Oxylebius pictus* also has both fundamental and socially modified sexual dichromatisms (DeMartini 1985).

Adult male and female *H. decagrammus,* like adult *O. pictus* (DeMartini and Anderson 1980, DeMartini 1985), segregate by habitat and depth in Puget Sound (Moulton 1977, Barker 1979). Perhaps intersexual competition for resources as well as sexual selection has contributed to the evolution of striking sexual dichromatisms in hexagrammids (DeMartini 1985).

Spawning Substrates

Most spawns of *Hexagrammos decagrammus* and all of the relatively few spawns of *H. stelleri* observed were laid on three-dimensional biological substrates. Rugose substrates probably provide more secure attachment sites for eggs and increased protection from oophagous fishes. Data are insufficient to evaluate whether any biological substrates are preferred over bare rock surfaces.

Egg Masses

The discrete nature of masses of *Hexagrammos decagrammus* and *H. stelleri* spawn, plus the usually distinct yolk coloration and developmental stage of each mass, strongly suggest that each mass is contributed by a different female. The sizes and average numbers of eggs present in *H. decagrammus* and *H. stelleri* spawns resemble those of several other similar-sized *Hexagrammos* spp. (Gorbunova 1970), which is consistent with this hypothesis. Each mass of eggs represents a female clutch in *Oxylebius pictus* (DeMartini and Anderson 1980). If this relation exists for *H. decagrammus* and *H. stelleri,* males often fertilize and tend the eggs of many females in multiple-clutch broods, as is typical for *Hexagrammos* spp. (Gorbunova 1970). Studies of female fecundity are needed to substantiate this for *H. decagrammus* and *H. stelleri.*

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The Effect of Antecedent and Ambient Salinity Levels on Seed Germination in Populations of *Carex lyngbyei* Hornem.

Abstract

The germination responses of four seed populations of *Carex lyngbyei,* an abundant sedge species in the intertidal marshes of the Pacific Northwest, were studied in relation to salinity. Germination only occurred in low-salinity conditions following after-ripening. Pre-germination exposure to high-salinity (20 ppt) conditions produced differential responses in the four populations. Augmentation of germination percentage by pre-germination exposure to high salinity occurred only in seed populations which were exposed to high-salinity conditions in the field prior to spring germination. No change in the speed of germination was observed as a result of exposure to variable salinity levels prior to germination.

Introduction

Carex lyngbyei is a clonal, perennial sedge that occupies a dominant position in estuarine marshes from northern California to Alaska (MacDonald 1977). It is abundant over a broad salinity gradient, from oligohaline to mesohaline, and over a wide elevational range (Jefferson 1975, Disraeli and Fonda 1979, Hutchinson 1982, Ewing 1983). Whereas the wide biogeographic range of a species such as *C. lyngbyei* may simply reflect the availability and accessibility (*via* oceanic dispersal) of suitable habitats, its ecological amplitude may indicate the extent of genetic divergence within the species. Divergence may be visibly expressed by morphological differentiation, or remain veiled, with intraspecific variation restricted to physiological traits. Bimodality of height forms (akin to the well-known case of *Spartina alterniflora* Loisel, dominant in the Atlantic marshes of North America [Anderson and Treshow 1980]) has been described in *C. lyngbyei* populations from several locations (Eilers 1975, Jefferson 1975, Levings and Moody 1976, Ewing 1982), but nothing is known of the physiological tolerances of the species or its subpopulations.

The most widely-examined, and likely most adaptively significant, variable physiological trait between and within maritime plant species is salt-tolerance. Paradoxically, seeds of most halophytic plants germinate best under freshwater conditions and at salinities below 5 ppt. Germination is reduced and delayed at salinities above 10 ppt, and at salinity levels equivalent to those of seawater (36 ppt) germination is negligible, even for highly salt-tolerant species (Ungar 1982). Therefore, halophytes do not differ markedly from glycophytes in their tolerance to salinity during germination. A more notable differentiating characteristic of halophytes is their ability to remain dormant at high salinities (when immersed in seawater for instance), and then germinate when conditions ameliorate. In addition, exposure to high salinity conditions serves to enhance germination percentages and germination speed in some halophytes (Binet 1964, 1965; Boorman 1967; Lesko and Walker 1969; Ungar and Hogan 1970; Ignaciuk and Lee 1980).

Intraspecific variation in salt tolerance of germinating seeds has been reported for several halophytic plants (McMillan 1959; Wells 1959; Dewey 1960; Cavers and Harper 1967; Workman and West 1967, 1969; Clarke and West 1969; Seneca 1972; Bazzaz 1973; Kingsbury *et al.* 1976; Antlfinger 1981). However, none of these studies deal directly with tolerance of, and response to, salinity conditions during the seed dormancy phase. Differentiation within a population for salt tolerance would likely be most marked in estuarine intertidal species such as *C. lyngbyei,* as estuarine habitats experience much more variable salinity regimes (in space and time) than other coastal environments.

In this and subsequent papers we propose to address the degree of ecotypic variation in *C. lyngbyei.* This study addresses a single question: to what extent is the rate and speed of germination in *C. lyngbyei* populations a function of ambient salinities during seed dormancy and the germination phase?

Materials and Methods

Field Sites

Carex lyngbyei plant material was collected from four sites in the estuarine marshes of southwestern British Columbia (Figure 1). The sites represent contrasting estuarine environments with distinctive annual river discharge and salinity regimes. Two sites were located on the Squamish River delta, situated at the head of a complex estuarine-fjord. The mountainous character of much of the Squamish drainage basin produces a discharge regime with a pronounced summer maximum resulting from snowmelt (Figure 2). In consequence, surface salinities in the estuary during the summer months are much reduced (Figure 3). The magnitude of the seasonal variation across the delta front depends upon distance from the active distributary and the estuarine circulation pattern. Levings *et al.* (1976) present data that demonstrate that surface salinity in the central part of the delta remains elevated (15-20 ppt) throughout the winter and declines rapidly in late spring to <5 ppt.

The Somass River delta is the bay-head delta of the long, narrow fjord known as Alberni Inlet. The Somass River is not primarily snow-fed, and its annual discharge regime more nearly parallels the annual precipitation pattern, with a mid-winter maximum and later summer minimum (Figure 2). Salinity observations published by Tully *et al.* (1957), Waldichuk *et al.* (1969) and Parker and Sibert (1972) indicate that the surface waters of Alberni Inlet remain brackish for a considerable distance from the delta front, generally remaining below 10 ppt throughout the year within 3 km of the river mouth. Birtwell (1978, and unpublished data) provides comparative information on salinity variation across the delta front (Figure 3b). His results demonstrate that freshwater (<0.5 ppt) conditions persist at the mouth of the Somass River for much of the observation period, whilst oligohaline conditions (<5 ppt) are maintained in the waters of Shoemaker Bay. During this time interval surface salinities in the western estuary were similar to those at Holm Island, for which a more extensive data record exists (Waldichuk *et al.* 1969). These latter data indicate that salinity variations throughout the year are much more uniform than those for the Squamish River estuary, with a maximum in late summer and early fall.

Plant material

Seeds of *C. lyngbyei* were collected in August 1983 from two populations in each delta representing the fresh and saline extremes of the

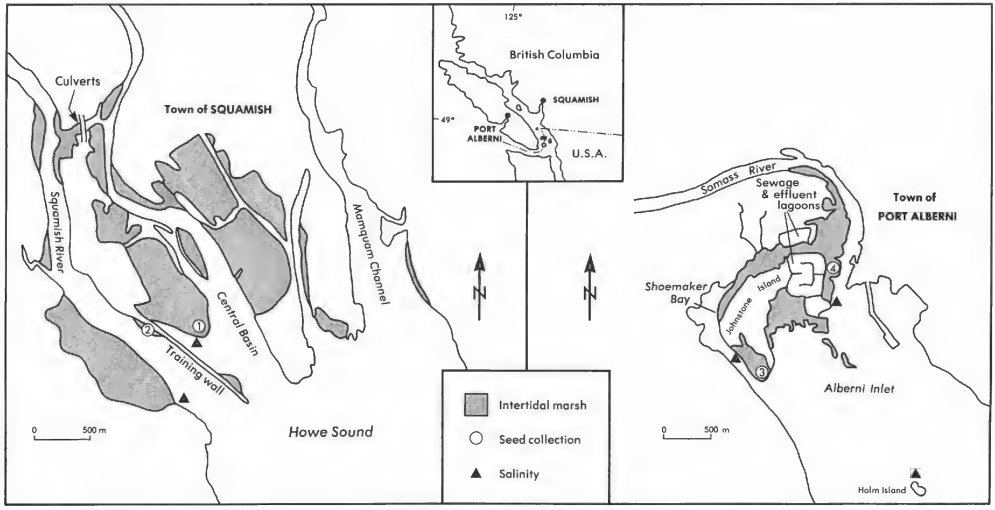

Figure 1. Location of the study sites, seed collection areas, and sites of salinity measurement.

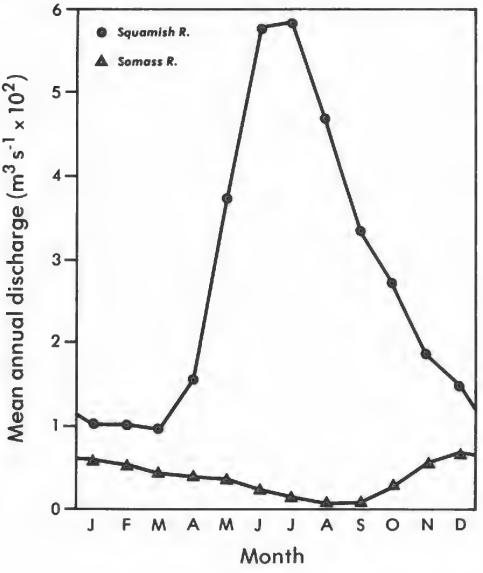

Figure 2. Mean monthly discharges for the Squamish and Somass Rivers. (Source: Environment Canada 1983: data for the Squamish-Cheakamus and Somass-Sproat gauging stations.)

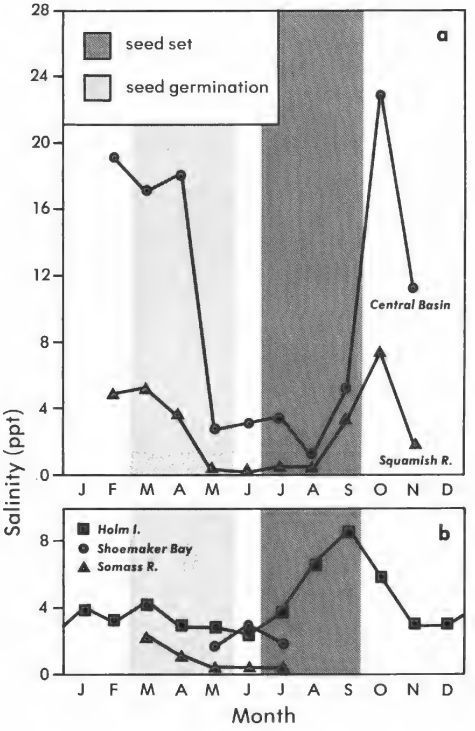

Figure 3. Annual salinity regimes for the a) Squamish and b) Somass estuaries. Data for the Squamish estuary are taken from Levings *et al.* (1976) and those for the Somass from Waldichuk *et al.* (1969) and Birtwell (1978 and unpublished data). Site locations are marked in Figure 1. Periods of seed set and seed germination are indicated.

delta-front salinity gradient. At Site 1 (Squamish, "saline") we collected 200 seedheads of *C. lyngbyei* sampled over an area of 1000 m^2 in a virtually monospecific stand of *C. lyngbyei*. Flowering shoots were relatively infrequent in this salt-stressed habitat, and some 50 percent of the seeds had been eaten by Lepidoptera larvae. Site 2 (Squamish, "fresh") was an 800 m^2 isolated patch of marsh bordering the main river channel. *C. lyngbyei* was dominant (70 percent cover), with an admixture of *Eleocharis palustris* (L.) R. & S. and *Juncus* spp. One hundred and fifty seedheads were collected over the entire marsh area. Seed production levels were higher, but predation levels were equivalent to those at Site 1.

Site 3 (Somass, "saline") was located in the marsh area adjacent to Shoemaker Bay. The vegetation here was more diverse than at any of the other sites; *C. lyngbyei* accounted for ~60 percent cover. A total of 160 seedheads were harvested over an area of 500 m^2. Site 4 (Somass, "fresh"), located on the west bank of the Somass River channel, was situated in an extensive *C. lyngbyei* stand with occasional patches of *Scirupus acutus* Muhl. Some 150 seedheads were collected from this locality over an area of 1000 m^2.

Germination experiments

All *C. lyngbyei* seeds were cleaned, rinsed in undiluted "Clorox" for approximately one minute, and stored dry for 2-3 days. All germination tests were made in 10 cm Petri dishes on two sheets of Whatman No. 1 filter paper moistened with 5 ml of solution. Fifty seeds were placed in an ordered array in each dish. Four replicate dishes were used per population. Dishes were inspected every 3 days and any water loss corrected by adding tapwater to the dishes. Germination (defined

as emergence of the radicle or plumule) was counted and seed removed every 3 days until day 12, then every 7 days. Solutions were produced by adding tapwater to seawater obtained from Burrard Inlet. Salinities were checked using a Y-S-I salinometer.

The salinity pretreatment comprised storage of the seeds in 0 ppt and 20 ppt salinity water in the dark for 100 days at 5°C ± 2°C. Seeds were then germinated at three salinity levels (0, 10, 20 ppt) in growth cabinets set on a 12 h photoperiod and 17°/8° thermoperiod. Light in the cabinets was supplied by "cool-white" fluorescent tubes producing ~1200 W m^{-2} at plant height.

In a further experiment, we attempted to germinate seeds at five salinity levels (0, 5, 10, 15, 20 ppt) without pretreatment.

The germination data were transformed to the arcsin square root of the germination percentage to stabilize the variance. The transformed data were subjected to hierarchical analysis of variance followed by Student-Newman-Keuls "*a posteriori*" multiple range tests. Mean time to germination (T) was calculated using the formula given by Ignaciuk and Lee (1980):

$$T = \Sigma DN/\Sigma N$$

where N is the number of seeds germinating in the interval between the previous count and day D.

Results and Discussion

None of the seeds in the experiment without seed pretreatment germinated. Seeds of *C. lyngbyei,* like those of all its temperate congeners (Andersen 1968), and most other temperate maritime plants, require after-ripening in order to germinate.

In the stratification-salinity pretreatment experiment no germination was observed at salinity levels of 10 ppt or above, and germination percentages in all freshwater treatments were less than 20 percent (Figure 4a). The ANOVA reveals significant differences between deltas, sites and pretreatments in terms of the magnitude of germination in freshwater. Immersion in a 20 ppt solution significantly reduced the germination percentage of seeds from Site 2 and significantly increased the germination percentage of seeds from Site 1 compared to freshwater immersion.

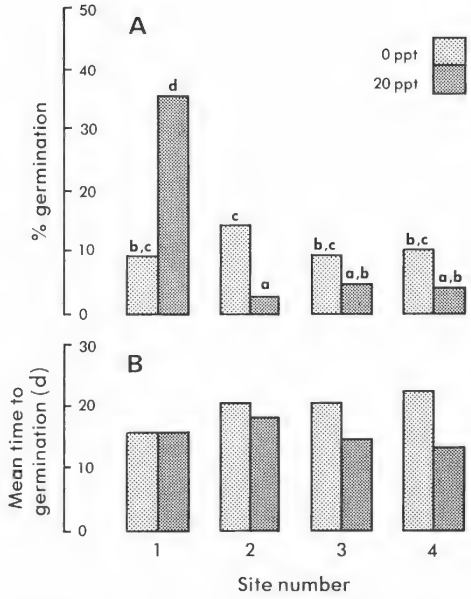

Figure 4. a) Mean germination percentages in fresh water and b) mean germination time in fresh water for seeds from four populations of *C. lyngbyei* following after-ripening in fresh (0 ppt) or saline (20 ppt) water.

In contrast, immersion in freshwater for an extended period of time produced no significant differences between seed populations in terms of germination percentage. Mean time to germination (Figure 4b) was also uniform for all seed populations.

Although *C. lyngbyei* seeds apparently germinate only in conditions of reduced salt stress, there is a strong intraspecific variation in germination response to antecedent conditions. If salinity levels are low during the phase of innate dormancy, all of the seed populations exhibit similar germination responses. However, if salinity levels are high (20 ppt) during dormancy, germination percentages may be augmented, reduced or remain unchanged. The response corresponds to the characteristic salinity regime of the seed provenance. Thus in the environs of Site 1, seawater-dispersed seeds derived from the local population clearly have an advantage over those (such as seeds from Site 2) which are inhibited by exposure to seawater.

TABLE 1. Analysis of variance of percentage germination (arcsin transformed) of *C. lyngbyei* seed from four populations in two deltas as a function of antecedent and ambient salinity.

Source	df	Mean Square	F ratio	Prob.
Deltas	1	0.0276	5.83	0.0175
Sites	2	0.0242	5.09	0.0086
Antecedent salinity	4	0.0331	6.97	0.0001
Ambient salinity	16	0.1609	33.91	0.0000
Error	72	0.0047		

Germination in winter and spring in the field is probably inhibited by low temperatures in all *C. lyngbyei* populations; the size of the germinating seedbank may be primarily a function of ambient and antecedent salinity. Seedling emergence takes place in the field from March to May (Hutchinson, unpublished data), during which time the salinity of the inundating water declines by an order of magnitude at all test sites. Emergence of *C. lyngbyei* seedlings may coincide with periods of heavy rain during this period; this serves to reduce interstitial salinity still further.

Local differentiation of wind-pollinated plant species such as *C. lyngbyei* does not require geographic discontinuity. Physiological and morphological microdifferentiation has been observed in self-incompatible wind-pollinated species over much shorter distances than those examined here (Jain and Bradshaw 1966, Silander and Antonovics 1979). Such microdifferentiation includes selection at the germination stage for salt tolerant biotypes (e.g. Cavers and Harper 1967); clearly there may be selection for tolerance of salinity conditions antecedent to germination as well.

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Insect Predation on *Astragalus Filipes* and *A. Purshii* Seeds

Abstract

Predispersal seed predation was measured during two growing seasons for *Astragalus filipes* Torr. and *A. purshii* Dougl. in eastern Oregon. Tortricid and weevil larvae were the primary seed predators on *A. filipes*. Larvae consumed 93 and 62 percent of the seed crop in 1980 and 1981, respectively. Pyralid larvae were the primary predators on *A. purshii* seeds. Forty-seven and 82 percent of the total seed crop survived predispersal predation in 1980 and 1981, respectively.

Introduction

An important role of legume seed predators in plant population biology may be their effect on natural colonization rates (Harper 1977). It may also be relevant to examine their effect on native seed reserves used for artificial recolonization.

While evaluating the feasibility of reestablishing original plant communities on deteriorated portions of the John Day Fossil Beds National Monument in eastern Oregon, fruits of many forb and shrub species were found to be preyed upon by insects. Available native seed sources were thereby severely reduced.

The magnitude of seed loss due to predators has been determined in only a few taxa. Lepidopterans (Ehrlich and Raven 1964, Breedlove and Ehrlich 1972, Green and Palmblad 1975), hemipterans (Green and Palmblad 1975), bruchids (Janzen 1969, Center and Johnson 1974), and cuclionid beetles (Platt *et al.* 1974) have been cited as avid legume seed predators.

A study was undertaken between 20 April and 25 June, 1980 and 1981 to (1) identify predispersal seed predators, (2) determine the extent of insect predation, and (3) note the stage of growth and season in which predation occurs on two native perennial *Astragalus* species. These species were chosen for study due to their relative importance in the undisturbed vegetation component.

This research was a cooperative effort and jointly supported by the USDI, National Park Service, John Day Fossil Beds National Monument and the Eastern Oregon Agriculture Research Center, jointly operated by the Oregon Agricultural Experiment Station and U.S. Department of Agriculture, Agricultural Research Service.

Study Area and Methods

Threadsilk milkvetch (*Astragalus filipes* Torr.), a tall herbaceous plant with numerous racemes and glabrous thin-walled pods, is found in the sagebrush zone of northern Nevada, southern Idaho and eastern Oregon (Barneby 1964). Woolly-pod milkvetch (*Astragalus purshii* Dougl.) is a low acaulescent taprooted plant with cottony pubescent pods. The latter species is variable and has many races within the Intermountain region of the western U.S. (Barneby 1964).

The study area was located within the John Day Fossil Beds National Monument in eastern Oregon. The steep rugged topography is dissected by the John Day River and the elevation ranges from 600 to 1200 m. The semiarid region has an average precipitation of 30 cm a year with the majority falling as rain during November through April. Average temperature for the spring-summer season is 15.5°C and 4°C for the fall-winter months. The vegetation, typical of the sagebrush biome, is dominated by Wyoming big sagebrush (*Artemisia tridentata* subsp. *wyomingensis* Beetle), western juniper (*Juniperus occidentalis* Hook.), and bluebunch wheatgrass (*Agropyron spicatum* (Pursh) Scribn. and Smith). Much of the area has been invaded by cheatgrass (*Bromus tectorum* L.) and broom snakeweed (*Xanthocephalum sorothrae* (Pursh) Shinners).

Three sites within the monument were chosen to study each of the two *Astragalus* species. On each study site 25 plants were randomly selected, tagged and numbered consecutively. The same sites were monitored in both years, but different individual plants were sampled each year. Each

site was visited at least once a week during the growing season, April through June. Phenology, number of flowers, number of nondamaged and damaged pods (those with a small hole in the pericarp) were recorded for each plant. Immediately prior to abscission, all of the damaged and nondamaged pods were collected and the number of seeds in each pod counted. Abortive fruits were not included in the seed total.

Seed potential/m^2 and actual seed survival/m^2 were determined for both species. Seed potential/m^2 was the product of the mean number of seeds per nondamaged pod and the mean number of pods/m^2. The mean number of seeds surviving per plant multipled by the number of plants/m^2 estimated actual seed survival/m^2. Percent seed success was estimated by dividing seed potential into seeds survived.

Three 10 m line transects (Canfield 1941) were used to measure cover of both *Astragalus* species on each site. All transects were located in relatively uniform areas. Rectangular plots, 20 x 50 cm, were placed at 1 m intervals on each transect to determine density. Plant density measurements were used to calculate seed potential/m^2 and seed survival/m^2.

Regression analysis were used to determine if seed predation level was related to the total number of pods per plant. Seed survival rates, the total number of flowers, undamaged pods and damaged pods per plant between 1980 and 1981 were compared using the Student t-test.

Larvae of insect predators were collected from fruits of nearby *Astragalus* plants and preserved in 70 percent ethanol. Additional larvae were reared into adults for identification. Other insects observed on *Astragalus* species were collected and later mounted and appropriately labeled. Specimens were identified and stored at the Oregon State University Entomology Museum.

Results

In 1980 and 1981, *A. filipes* pods were attacked by microlepidopteran larvae (*Torticidae*). Weevil larvae (*Curculionidae*) were also found in the seed pods in 1981. No attempt was made to distinguish damage caused by the two insect granivores.

In 1980, predation within *A. filipes* pods was initiated shortly after 15 May (Figure 1), and within 15 days evidence of pod entry was recorded in over 80 percent of the fruits. No further predation occurred after mid-June. In 1981, both pod development and active seed predation occurred over a longer time span.

The percent of seed crop consumed by insects decreased from 1980 to 1981 (Figure 1). Less than 7 percent of the potential seed crop survived predispersal insect predation in 1980, whereas almost 38 percent of the seed survived in 1981. Athough the numbers of damaged pods per plant increased in 1981, the total number of pods per plant increased and proportionately fewer pods were damaged (Table 1).

Green and white microlepidopteran larvae of the family *Pyralidae* were observed in *A. purshii* pods. Adult pyralid moths were not observed ovipositing, but eggs were found attached to the pericarp of the pods. Larvae bored holes through the immature pods and consumed developing

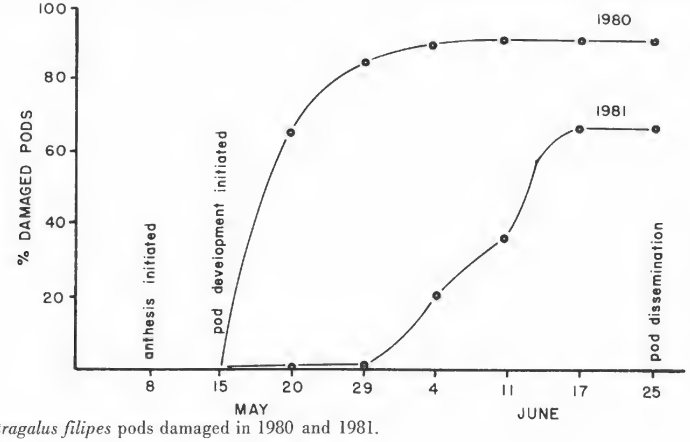

Figure 1. Percent *Astragalus filipes* pods damaged in 1980 and 1981.

Table 1. Means ± sd for plant density, seed pods per plant, number of seeds per pod, total seeds developed per m² and actual seeds per m² escaping predispersal insect predation.

	Plants/ m²	Flower/ plant	# pods/ plant	# damaged pods/plant	# seeds/ pod	Seeds[1] produced/m²	Seeds[2] survival/m²
Astragalus filipes							
1980	1.33±.1	126±21	16±4.8*[3]	15±4.5*	2.0±1.1	43±12.4*	3±.9*
1981	1.33±.1	152±18.5	40±6.7	26±4.5	3.8±2.0	202±50.5	76±19
Astragalus purshii							
1980	2.0±1	27±3.2	6±.9*	3±.6*	8.0±3.8	96±35.5	45±16
1981	2.0±1	24±0.6	4±.7	.7±.3	7.4±3.7	59±23	48±19

[1](Plant/m²)•(#pods/plant)•(#seeds/pod)
[2](Seeds produced/m²)•(% seed survival)
[3]Means within species and plant parameter are significantly different ($p < .10$) between years.

seeds. In most pods, larvae fed on all seeds within the fruit. No pupae were found in the pods, therefore, it was assumed pupation occurred in the soil.

Astragalus purshii fruits were developing and pryalid eggs were observed by early May (Figure 2). By 12 June the number of damaged pods had peaked. Active seed predation and phenology of *A. purshii* pods was observed over the same period of time in 1980 and 1981.

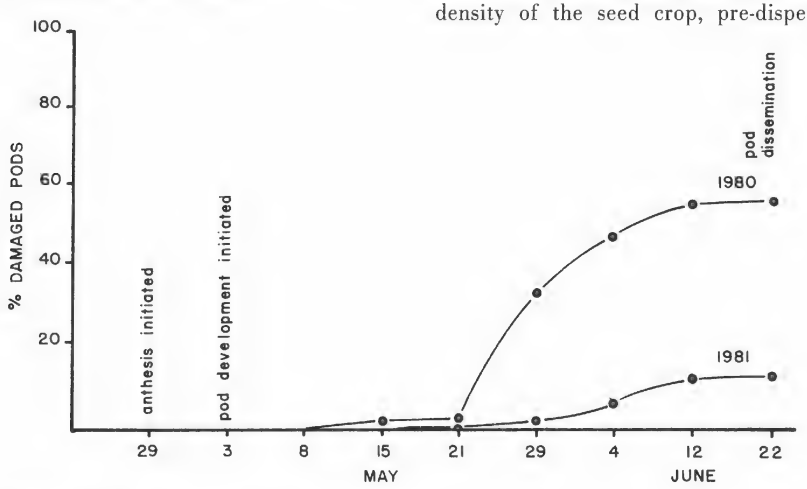

Figure 2. Percent *Astragalus purshii* pods damaged in 1980 and 1981.

Fewer seed pods of *A. purshii* were preyed upon in 1981 (Table 1). Forty-seven percent of the seed crop survived in 1980 and 82 percent in 1981. Both the total number of pods and the number of damaged pods decreased in 1981. However, the number of damaged pods showed a greater decrease. As in *A. filipes* the number of damaged pods on individual *A. purshii* plants within years increased proportionately with total number of pods per plant.

Discussion

Insect seed predators were associated with large reductions in seed crops of *A. filipes* and *A. purshii.* In both species the number of flowers per plant was not significantly different between years. However, the total number of pods on an individual plant significantly increased in *A. filipes* and decreased in *A. purshii* in 1980 and 1981, respectively. The proportion of total seed pods damaged decreased in 1981 for both species.

The impact of seed losses may vary from species to species (Crawley 1983). Both *Astragalus* are perennials not dependent on current seed production. Long-lived seed banks, repeated reproduction and mixed-age stands enable these species to persist (Cohen 1968). However, seeds are the major means of higher plant dispersal and colonization (Silvertown 1982). By reducing the density of the seed crop, pre-dispersal seed predators alter the pattern of seed dispersal. The distance in which successful natural colonization may occur is reduced (Harper 1977).

Many other factors also reduce the potential for natural colonization of native species on our western rangelands. Undisturbed stands of native communities are few and far between. Exotic species often outcompete the natives for available soil moisture (Harris 1967). Some means of artificial reseeding is necessary to enhance these native species' survival and to return these lands to optimum productivity. Due to insect seed predation, dependence on wild seed sources for revegetation efforts is probably inadequate and unreliable.

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Zooplankton Grazing Activity and Assimilation in the Presence of Mount St. Helens Ash

Abstract

Experiments were conducted to determine the effects of the particulate fraction of Mt. St. Helens ash on ingestion rate, filtration rate, and assimilation efficiency of *Diaptomus ashlandi* Marsh and *Daphnia pulex* Leydig. When fed *Cryptomonas* together with ash, grazing activity by both zooplankters, was not affected. When fed *Cyclotella* with small amounts of ash, *Daphnia* ingested more algae whereas *Diaptomus* did not. Ash interfered with the assimilation of carbon-14 by *Daphnia* ingesting *Cyclotella.*

Introduction

The volcanic eruption of Mt. St. Helens on 18 May 1980 produced tons of ash and debris to be carried eastward by prevailing winds. More than 30 lakes in the immediate vicinity of the eruption sustained altered physical, chemical, and biological characteristics because of ash deposition (Dion and Embrey 1980). The ash was deposited in various amounts over Washington, Idaho, Oregon, and Montana (Sarna-Wojcicki *et al.* 1980), suggesting that surface waters of the Pacific Northwest will contain suspended ash particles for many years to come. Seasonal runoff and sediment mixing are primary factors determining the amount of ash that will be present in the water column, and particles less than 20 μm in diameter are likely to remain suspended for long periods.

Frutcher *et al.* (1980) have characterized both the particulate and soluble fractions of the ash, whereas Pereira *et al.* (1982) focused on organic contaminants. Of course, filter-feeding zooplankton may be directly affected by the particulates because of the nature of their feeding mechanism. Furthermore, increases in the ash-phytoplankton ratio may alter the ingestion rate through selectivity, as well as the assimilation efficiency by changing physical and chemical properties of gut contents. Many investigators have studied zooplankton preference for both large cells (Burns 1968, 1969a; Hargis 1977; Arnold 1971) and small cells (Hadas 1982, Burns 1969b, Vanderploeg 1981) in order to clarify the complex pattern of particle size selection, a pattern that could be altered in the presence of ash particles. Although dissolved components are many, virtually all of the ash is insoluble in water. In this study we examined the particulate fraction of Mount St. Helens ash for its effects on filtration rate, ingestion rate, and assimilation efficiency of two filter-feeding zooplankters, *Diaptomus ashlandi* Marsh and *Daphnia pulex* Leydig, using *Cylotella meneghiniana* Kütz, a 500 μm^3 centric diatom, and *Cryptomonas ovata* Ehr., a 1000 μm^3 ovoid flagellate as food sources.

Methods

Mount St. Helens ash, collected 18 May 1980 at Pullman, Washington, was used in experiments after 10 g l^{-1} was allowed to settle undisturbed in deionized distilled water at 20°C for 72 h. The ash suspension was then removed from settled material by siphoning and filtered through a 0.2 μm - 24 mm membrane. The ash/filter cake was washed copiously with distilled water and concentrated by backflushing the ash with synthetic medium (Rees 1979). A mean concentration was determined by vacuum drying five 1-ml samples at 65°C for three h then weighing. The concentrated suspension ($\sim$1.9 mg ml^{-1}) was stored at 5°C in the dark for approximately one week before using.

Cyclotella meneghiniana Kütz (clone CyOH2 obtained from S.S. Kilham) and *Cryptomonas ovata* Ehr. (Texas Culture Collection UTEX #358) were maintained in Rees's medium at 20°C with a photoperiod of 15L:9D under 0.35 ly h^{-1} of cool white fluorescent light. Algal cell cultures were acclimatized to the appropriate light temperature conditions for 24 h prior to experiments.

Daphnia pulex Leydig and *Diaptomas ashlandi* Marsh were collected from Rock Lake, Washington, and maintained in Rees's medium at 14°C with a light flux of 0.70 ly h^{-1}. All experiments concerning the ash-zooplankton interaction were carried out under 0.70 ly h^{-1} at 8°, 14°, and 20° C unless noted overwise. Experimental animals were acclimatized to their respective test temperatures for 14 days to allow stabilization of metabolic activity (Hargis 1977). *Cyclotella* was supplied weekly as a primary food source, but bacteria and other algal contaminants likely were also present. Male and female (gravid or non-gravid) animals were selected at random for all experiments.

Algal cells were labeled radioactively by adding 50 ml of 1 μCi ml^{-1} ^{14}C-$NaHCO_3$ to 100 ml of culture. The cultures were placed under continuous 1.40 ly h^{-1} illumination for 48 h at 20°C, then harvested by centrifugation, washed three times, and resuspended in Rees's medium. The cells were incubated overnight at the test temperatures prior to experiments. Triplicate 20-ml samples were filtered, digested, and counted to determine mean specific activity.

For *Diaptomus* or *Daphnia,* the effects of particulate ash on ingestion rate, filtration rate, and assimilation rate were tested using four concentrations of ash (0, 10, 50, and 250 mg l^{-1}) mixed with labeled unialgal suspensions of *Cryptomonas* or *Cyclotella.* The four grazing experiments (2 zooplankton species x 2 phytoplankton species) were replicated six times. The procedure involved placement of 20 diaptomids or 10 daphnids in 125-ml Erlenmeyer flasks containing 25 ml Rees's medium for 15 h prior to experiments. No food was provided during this period. Then 20 ml of the labeled algal suspension were added while simultaneously adding concentrated ash. Rees's medium also was added to bring the final volume to 60 ml. Each replicate consisted of 12 flasks (4 ash concentrations x 3 temperatures).

The feeding times in labeled-cell suspensions were critical. Test periods should be shorter than the time to first egestion of labeled cells (Richman 1966, Schindler 1968, and Kibby 1971). Hargis (1977) provided a time-course study for *Diaptomus ashlandi* showing 30 min to first egestion. In our experiments, the animals were allowed to feed for 10 min as suggested by Krylov (1981). One half of the number of animals present in each flask was then removed by pipette and filtered onto GF/C glass fiber filters. Each filter was placed in a scintillation vial to which 1 ml of tissue solublizer was immediately added. After 24 h digestion, the samples were counted to estimate ingestion. The remaining animals were placed into unlabeled cell suspensions of the same concentration. After feeding for 5 h, they were removed by filtering with Nitex mesh, digested, and counted. The assimilation efficiency was estimated by calculating the ratio of animal radioactivity after 5 h of gut clearance to the total radioactivity ingested in 10 min. Filtration rates were estimated by the equation:

$$FR = \frac{\text{dpm mg}^{-1}}{\text{dpm ml}^{-1}} \times \frac{60 \text{ min h}^{-1}}{\text{T min}}$$

where FR is filtration rate (ml mg^{-1} h^{-1}) and T is duration of the labeled feeding period. The ingestion rate (cells mg^{-1} h^{-1}) is the product of food density (cells ml^{-1}) and FR. Food density (cells ml^{-1}determined by averaging 10 haemocytometer counts) was kept between 25,000-500,000 which is reported to produce a constant ingestion rate (Richman 1966). Live and dead animal controls for self-absorption of radioactivity were considered to be insignificant as reported in similar feeding experiments (Richman 1966).

Results and Discussion

Ash Characterization

The composition of ash used in experiments and characterized by x-ray fractionization (Geology Department, Washington State University) was SiO_2-67.0, Al_2O_3-17.1, TiO_2-0.6, Fe_2O_3-1.9, FeO-2.1, MnO-0.1, CaO 4.3, MgO-1.6, K_2O-1.6, $Na_2O-3.6$, P_2O_5-0.2 percent. Settling reduced the suspended particulate fraction to approximately 30 mg l^{-1}, 96 percent of the particles with volumes less than 9μm. Microscopic examination of water samples from nearby lakes revealed the presence of many particles larger than those left in laboratory suspensions, suggesting that re-suspension caused by wind and currents is common.

Grazing by Zooplankton

Table 1 presents mean filtration, ingestion, and assimilation rates over all treatments (ash level, temperature) for each replicate by experiment. Although chemical and physical conditions were virtually constant among replicates, variability within experiments still was very high. Clearly,

TABLE 1. Mean filtration (ml mg^{-1} h^{-1}), ingestion (10^5 cells mg^{-1} h^{-1}), and assimilation percentage for each replicate.

Experiment	Replicate 1	2	3	4	5	6
Diaptomus-Cryptomonas						
Filtration	17.6	18.1	6.2	5.7	5.2	2.9
Ingestion	5.4	5.6	2.4	2.2	2.0	1.1
Efficiency	20.1	28.8	27.4	36.2	30.4	53.0
Daphnia-Cryptomonas						
Filtration	13.1	12.3	1.0	.7	13.3	14.9
Ingestion	9.8	8.9	.3	.2	6.8	7.6
Efficiency	63.0	78.4	61.9	79.3	31.4	31.9
Diaptomus-Cyclotella						
Filtration	10.5	9.0	33.7	60.6	4.3	4.6
Ingestion	4.6	3.9	1520.0	2740.0	61.8	66.0
Efficiency	51.0	55.5	29.1	26.2	44.3	30.7
Daphnia-Cyclotella						
Filtration	.2	.3	10.6	11.4	6.4	5.6
Ingestion	.6	.8	41.4	44.5	64.8	56.6
Efficiency	38.4	30.2	24.5	28.3	20.5	27.6

condition of the algal food, as well as animal age and size, may affect grazing activity. For example, daphnids feeding on cryptomonads in replicates 3 and 4 were much smaller than those utilized in other replicates (Table 2), and there are substantial differences in filtration and ingestion rates. These results are contrary to those

TABLE 2. Mean animal dry weight (μg) by feeding experiment for each replicate.

Experiment	Replicate 1,2	3,4	5,6
Diaptomus-Cryptomonas	14.0	3.1	6.1
Daphnia-Cryptomonas	1950.0	10.9	94.0
Diaptomus-Cyclotella	14.0	3.1	5.2
Daphnia-Cyclotella	17.5	24.1	5.0

of Burns (1968, 1969b). Also, the small copepods used to test for effects of particulate ash when fed *Cyclotella* were considerably more active than the larger animals used in replicates 1 and 2 (Table 1).

Replicate variability was removed by making all observations for a given replicate relative to the mean for that replicate. The subsequent analyses of variance are summarized in Table 3. Although there were six replicates for each experiment, only one light flux (0.70 ly h^{-1}) was used at each of the three experimental temperatures. Consequently, 56 degrees of freedom were available for the error term in analysis of variance (ANOVA) tests of significance.

TABLE 3. Analysis of variance (F-values) for feeding experiments: #1 *Diaptomus-Cryptomonas* (See Table 4), #2 *Daphnia-Cryptomonas*, #3 *Diaptomus-Cyclotella* (see Table 5), #4 *Daphnia-Cyclotella* (see Table 6). Error term has 56 degrees of freedom.

Effect	d.f.	Experiment # 1	2	3	4
Filtration or Ingestion					
Ash (A)	3	2.62	.41	1.34	3.49*
Temperature (T)	2	.74	.73	2.94	4.28*
A x T	6	.79	.64	1.03	1.24
Assimilation					
Ash (A)	3	.32	1.19	.93	3.46*
Temperature (T)	2	1.69	.51	3.18*	.70
A x T	6	.76	.69	1.83	.73

* $P < .05$

Diaptomus-Cryptomonas (Experiment #1)

Since food concentration was the same for all treatments within each replicate, ingestion rate is always a constant times filtration rate and ANOVA results are the same for both. No consistent effect of particulate ash was detected for filtration/ingestion nor was a significiant effect found for assimilation (Table 3) There is the suggestion of a temperature effect on filtration/ingestion (Table 4), perhaps highest at 14°C ($P \sim .06$).

TABLE 4. Relative filtration, ingestion, and assimilation of *Cryptomonas* by *Diaptomus* in the presence of particulate ash (means for six replicates).

	Temperature (°C)	Particulate Level (mg l^{-1}) 0	10	50	250
Filtration or Ingestion	8	1.02	.58	1.15	.78
	14	1.19	1.33	1.22	.98
	20	1.00	.89	.91	.90
Mean		1.07	.93	1.09	.90
Assimilation	8	1.47	1.50	.91	.90
	14	1.11	.77	.93	1.09
	20	.70	.88	.81	.93
Mean		1.09	1.05	.88	.97

Daphnia-Cryptomonas (Experiment #2)

No evidence for an effect of ash on cryptomonad grazing by *Daphnia* was found and none is supported by ANOVA (Table 3). Apparently the presence of ash did not influence the feeding behavior of *Daphnia.*

Diaptomus-Cyclotella (Experiment #3)

Temperature apparently affected assimilation rate, with highest values at 14°C (Tables 3 and 5). There was also the suggestion of a temperature effect on filtration/ingestion, but as with experiment 2, ash particles did not alter grazing activity.

TABLE 5. Relative filtration, ingestion, and assimilation of *Cyclotella* by *Diaptomus* in the presence of particulate ash (means for six replicates).

	Temperature (°C)	Particulate Level (mg l^{-1}) 0	10	50	250
Filtration or Ingestion	8	1.38	1.22	1.62	.63
	14	.74	.69	.88	.76
	20	.76	.95	1.24	1.14
Mean		.96	.96	1.25	.84
Assimilation	8	.77	.87	1.10	1.13
	14	1.89	1.12	1.01	1.89
	20	.92	.95	.61	.74
Mean		1.19	.98	.91	.92

Daphnia-Cyclotella (Experiment #4)

Filtration/ingestion was affected by both temperature and by ash (Tables 3 and 6). The highest rates occurred at 20° C and at intermediate ash concentration. Assimilation, on the other hand, was only affected by the presence of ash. Here the ash particles apparently interfered with assimilation in that the rate at the highest ash level was reduced to approximately half of that measured when no ash was present (Table 6).

Two additional experiments, in triplicate, were run at 14°C using *Daphnia* in an effort to support these results; one experiment involved *Cryptomonas* and the other experiment involved *Cyclotella.* Ash levels used were as before. This time, at one temperature, assimilation of both *Cryptomonas* and *Cyclotella* was adversely affected by the ash (Table 7).

TABLE 6. Relative filtration, ingestion, and assimilation of *Cyclotella* by *Daphnia* in the presence of particulate ash (means for six replicates).

	Temperature (°C)	Particulate Level (mg l^{-1}) 0	10	50	250
Filtration or Ingestion	8	.88	1.15	.97	.69
	14	.64	.90	.97	.93
	20	.93	1.28	1.72	.93
Mean		.82	1.11	1.22	.85
Assimilation	8	1.32	1.31	1.23	.61
	14	1.44	.93	.65	.77
	20	1.26	.90	.78	.82
Mean		1.34	1.05	.88	.73

TABLE 7. Relative filtration, ingestion, and assimilation by *Daphnia* at 14°C.

	Particulate Level (mg l^{-1}) 0	10	50	250
Cryptomonas				
Filtration of Ingestion	.71	1.06	1.00	1.23
Assimilation	1.29	1.08	1.04	.59
Cyclotella				
Filtration or Ingestion	1.04	1.11	1.05	.81
Assimilation	1.18	1.00	.80	.94

There is a wealth of literature dealing with filtration and associated assimilation by microcrustaceans feeding on phytoplankton in the absence of inert particles (Wetzel 1983). In general, our values fall within the range of reported results, although some extremely high rates of filtration were observed for *Daphnia* feeding on *Cyclotella* (Table 1). Closer to our objectives, Edmondson (1984) reviewed broadly the many possible effects of volcanic ash in lakes, hence a lengthy discussion here would be redundant. He does point out, however, that some species of *Daphnia* are able to live for long periods in ponds made turbid by silt and clay. Furthermore, crustaceans and rotifers in Soap Lake and Lake Lenore, Washington, carried on with their normal seasonal changes following heavy ash fall (Edmondson and Litt 1984). It is not surprising, therefore, that grazing in our

study by *Diaptomus* and *Daphnia* on *Cryptomonas* was not altered significantly by the presence of particulate ash, a conclusion that applies equally to *Diaptomus* feeding on *Cyclotella.*

Mechanisms responsible for these limited effects have not been identified, although ash particles ingested with phytoplankton probably would reduce assimilation by limiting the amount of digestible algal material in contact with the gut wall. Further speculation suggests that intermediate ash concentrations might increase filtration in response to metabolic demand, whereas very large concentrations might cause *Daphnia* to avoid these foreign particles, thereby overriding demand.

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Root Competition in a Low-elevation Grand Fir Forest in Montana: a Trenching Experiment

Abstract

Plots were trenched in an old-growth bottomland grand fir, *Abies grandis,* forest in western Montana. Cover and density of herbaceous species increased throughout the first five years in the trenched plots as contrasted with untrenched control plots. The release of the undergrowth by trenching demonstrates the importance of root competition, presumably for moisture and nutrients, in suppressing the undergrowth in these forests.

Introduction

Shady forest floors that are nearly barren of plants are common in the mesic coniferous forests of the Pacific Northwest. One's first impression, that light is limiting the undergrowth (herb and shrub layers), may be misleading. Trenching experiments in eastern North America (Toumey and Keinholz 1931, Korstian and Coile 1938) and Europe (Fricke 1904, Fabricius 1927) suggest that root competition may be more strongly limiting than light under dense canopies. These experiments release undergrowth from root competition by trees. A trench is dug around a plot, severing all roots, then the trenches are refilled. Soil moisture and nutrients (nitrate and ammonium, Vitousek 1977) in the plot increase because of reduced uptake by surrounding trees, and the effect of this treatment on the undergrowth is observed for several years. These experiments have shown that root competition inhibits the undergrowth.

I established trenched plots at two locations in western Montana to see if similar results would be obtained in closed-canopy bottomland conifer forests. On these sites a high water table could possibly ameliorate the water stress on the forest floor by providing an abundant supply for trees and perhaps shrubs and herbs.

Methods

Two pairs of similar control and treatment plots (2 x 2 m) were selected at a moist bottomland site with suppressed undergrowth at the University of Montana Biological Station (47°52'35''N, 114°01'50''W) on Flathead Lake. The stand was on soil developed from sandy and gravelly alluvium. The site was dominated by grand fir (*Abies grandis*), with occasional western larch (*Larix occidentalis*) and douglas fir (*Pseudotsuga menziesii*); nomenclature follows Hitchcock and Cronquist (1973). The shrub, herb, and bryoid layers were species poor and low in cover. Beadlily (*Clintonia uniflora*) and Hooker fairy-bell (*Disporum hookeri*) were the most prominent undergrowth species. No plots were beneath canopy gaps and all were similar in species composition and total cover at the outset. Plots were nearly level and contained no trees. Control (untrenched) and trenched plots were close to one another (>3 m and <15 m apart).

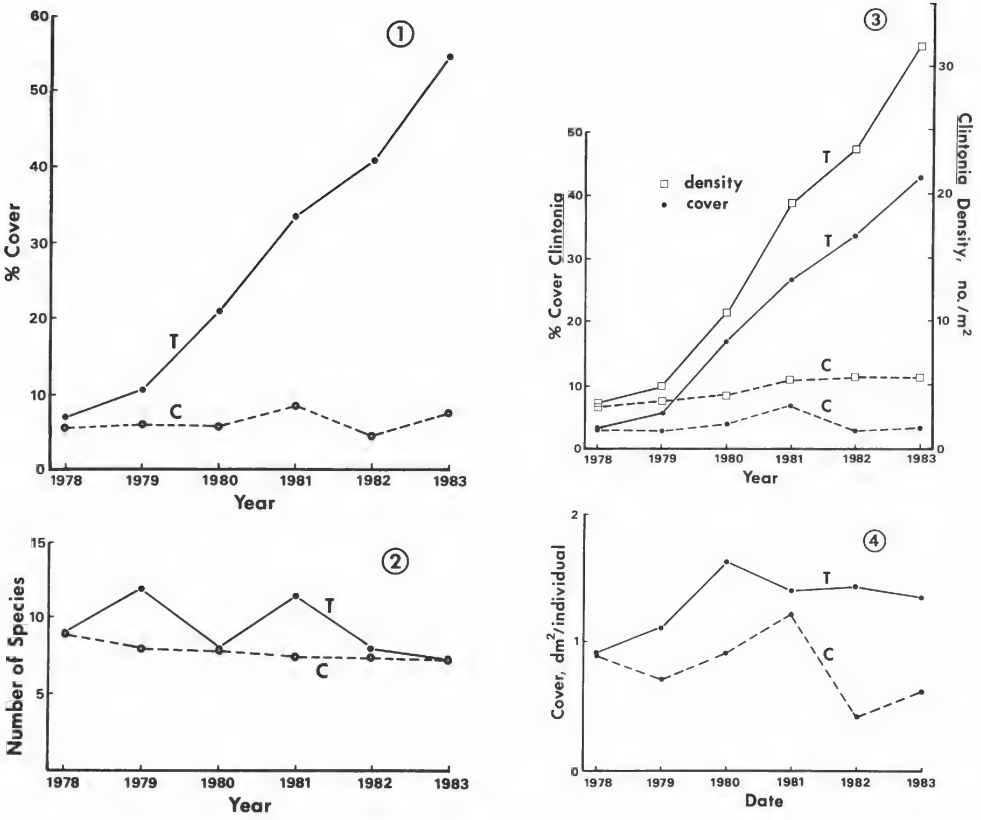
Trenches were dug in July, 1978 to a depth of 0.5 m on the perimeter of the plots. This severed most roots entering or leaving the plot, as most roots were in the top 0.3 m of soil. The plot sides of the trenches were lined with 4 mil polyethylene, then the trenches were filled. While trenches were being dug, soil was piled on plastic sheets adjacent to the plots. Corners were permanently marked with 0.5 m sections of 1 cm steel rods.

Cover of each plant species was recorded in midsummer (between 9 July and 4 August) by visual estimation in each 1 x 1 m quarter of each plot. Density was also recorded for those species whose individuals are relatively distinct. Data were collected each year from 1978 through 1983.

Results and Discussion

Overall Response

Total plant cover increased from 7 percent (1978) to 55 percent (1983) in the trenched plots, while cover in untrenched control plots remained relatively constant at about 6 percent for the five-year period (Figure 1). The response to trenching was similar in both Flathead Lake plots.



Figures 1-4. Changes in trenched (T) and control (C) plots at Flathead Lake from 1978 through 1983. 1. Total percent cover. 2. Plant species richness. 3. Cover and density of *Clintonia uniflora*. 4. Average cover of individual ramets of *Clintonia uniflora*.

The number of species showed little overall change on both trenched and control plots at both sites. However, trenched plots at Flathead Lake showed greater fluctuations from year to year than did control plots (Figure 2). These fluctuations (net loss or gain of 3-4 species per year) resulted mainly from fluctuations in seedling establishment and survival: seedlings observed in one year were commonly absent the next.

Components of Response

Changes in overall cover and density on the plots can be broken down into several aspects of population dynamics: (a) changes in the size of individuals resulting from growth and environmental fluctuations, (b) recruitment of new individuals, and (c) mortality. Each aspect is considered below. Since changes in the abundance of *Clintonia uniflora* accounted for most of the increase in cover on trenched plots, it is the focus of the following analysis of population dynamics.

Changes in size of individual ramets. The increase in cover of the most abundant species, *Clintonia uniflora* (Figure 3), was partly due to the production of more above-ground leaf area from existing ramets. Average cover of individual ramets on trenched plots rose from 0.9 dm^2 in

1978 to a peak of 1.6 dm^2 in 1980, then declined to 1.3 dm^2 by 1983 (Figure 4). The drop in average size after 1980 may reflect the increase in density of small first- and second-year *Clintonia* ramets. By contrast, average cover of individual *Clintonia* ramets on control plots fluctuated between 0.7 and 1.2 dm^2, then fell to near 0.5 dm^2 in 1982 and 1983 (Figure 4). These fluctuations apparently were caused by changes in the leaf area of individual ramets, assuming that mortality and recruitment of ramets were negligible.

Recruitment. In the first year after trenching, density of *Clintonia* ramets at Flathead Lake was nearly unchanged. Since then, density increased at a fairly constant rate of 5-8 ramets/m^2/yr (Figure 3), a rapid increase considering the low starting densities of < 10 ramets/m^2. Density of *Clintonia* remained nearly constant in the control plots.

Mortality. Because individuals were not marked and followed, mortality can only be inferred from fluctuations in density. Fluctuations in numbers, and hence probably mortality, of the major herbaceous species were small in both control and trenched plots. There were, however, pronounced fluctuations in shrub and tree seedlings in both control and treatment plots. First-year seedlings of Rocky Mountain maple (*Acer glabrum*), serviceberry (*Amelanchier alnifolia*), *Abies grandis,* and *Pseudotsuga menziesii* were frequently found, although very few of these survived a second year. Leaves on the shrub seedlings were often partly eaten, suggesting that herbivory may account for much of their mortality.

This experiment shows that root competition, presumably for water and nutrients, can limit the development of herbs beneath a full coniferous canopy, even on moist alluvial bottomlands. While this experiment suggests an important role of root competition in limiting the undergrowth, it does not imply that light, allelopathy, or other factors are not important.

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Identification of the *Artemisia Tridentata* ssp. *Wyomingensis/Festuca Idahoensis* Habitat Type in Eastern Oregon[1]

Abstract

Six stands of the *Artemisia tridentata* ssp. *wyomingensis/Festuca idahoensis* (ARTRW/FEID) habitat type were assessed for vegetation and soils information. *Festuca idahoensis* was the dominant understory species with frequency values ranging from 16.7 to 100%. *Poa sandbergii, Sitanion hystrix* and *Stipa thurberiana* were common associates in this habitat type. *Bromus tectorum* was most prevalent on sites with coarse textured soils. Soil textures ranged from silt loam, sandy loams and loamy sands. The distribution of *Artemisia tridentata* ssp. *wyomingensis/Festuca idahoensis* habitat type appears unique to Oregon.

Introduction

In eastern Oregon, approximately 10,000,000 hectares of rangeland support sagebrush/grassland vegetation (Winward 1980). The most common woody species on these sites, Wyoming big sagebrush (*Artemisia tridentata* ssp. *wyomingensis*), is considered more xeric than other members of the big sagebrush group. Although habitat types dominated by Wyoming big sagebrush have been recognized, classification of these plant communities has primarily been developed in other regional areas. The most comprehensive evaluations have been performed in Idaho. Common understory associates which have been used to delineate habitat types include: bluebunch wheatgrass (*Agropyron spicatum*), Thurber's needlegrass (*Stipa thurberiana*), needle-and-thread (*Stipa comata*), Sandberg bluegrass (*Poa sandbergii*), and squirreltail (*Sitanion hystrix*) (Winward 1970, Hironaka and Fosberg 1983).

Although sagebrush dominated lands in Oregon are similar to those encountered in Idaho, one plant community not described is the *Artemisia tridentata* ssp. *wyomingensis/Festuca idahoensis* (ARTRW/FEID) association. Generally, Idaho fescue (*Festuca idahoensis*) has been associated with the more mesic portions of the region and has not been reported to occur in conjunction with the relatively xeric Wyoming big sagebrush (Hironaka and Fosberg 1983). It is important for land managers to be aware of this habitat type when resource-use plans are formulated for sagebrush grasslands. The purpose of this report is to describe the vegetation and soils in the ARTRW/FEID habitat type.

Materials and Methods

In order to clarify synecological relationships which exist within the ARTRW/FEID habitat type, six stands were located in eastern Oregon and sampled for vegetation and soil characteristics. Three of the sites were situated near Baker (B_1, B_2, and B_3), two at Squaw Butte Experiment Station west of Burns (S_1 and S_2) and one in close proximity to Hampton (H_1). Site locations are given in Table 1.

The following procedures, modified from Poulton and Tisdale (1961), were used to gather vegetation information. At each site, a circular macroplot with a 25 m radius was empirically located so as to be representative of the plant species present within the stand. Through the center of each plot, a randomly located baseline was established. During the summer of 1980 three 30 m X 1 cm transects at distances of 8 and 16 m on one side of the plot center and 8 m on the other side of the plot center were established perpendicular to the baseline. Along each transect at 3 m intervals, frequency of all plant species present was determined utilizing a

[1]This research was a cooperative effort and jointly supported by the USDA, Agricultural Research Service and Eastern Oregon Agricultural Research Center, Squaw Butte Station, Agricultural Experiment Station. Tech. Paper No. 6630, Oregon Agricultural Experiment Station.

TABLE 1. Site descriptions and soil information for six eastern Oregon stands of *Artemisia tridentata* ssp. *wyomingensis/Festuca idahoensis* habitat type.

	Stand					
	B[1]	B[2]	B[3]	S[1]	S[2]	H[1]
County	Baker	Baker	Baker	Harney	Harney	Deschutes
Township and Section	9S 21(NE¼NE¼)	9S 27(NE¼NE¼)	8S 7(SW¼SE¼)	23S 34(SE¼NE¼)	24S 22(SE¼NW¼)	21S 33(SW¼NW¼)
Range	41E	41E	41E	25E	25E	21E
Elevation (meters)	1100	1100	1100	1341	1432	1341
Aspect and Percent Slope	NE8	W10-15	N3	N2-4	E2	N5-10
15 Year Precipitation Average (1962-1977) cm/yr		26.2			26.7	24.9
Soil Family	Xerollic durorthid clayey/sandy skeletal, fr.	Xerollic durorthid fine loamy, frigid	Haploxerollic durorthid coarse loamy, frigid	Xerollic durorthid coarse loamy, frigid	Aridic durixeroll coarse loamy, frigid	Xerollic durorthid fine frigid
Soil Depth to Restrictive Horizon (cm)	31	42	48	51	76	61
Soil Surface: Texture	Silt Loam	Silt Loam	Silt Loam	Sandy Loam	Sandy Loam	Loamy Sand
pH	7.4	7.4	7.0	7.2	6.7	7.2
% OM	1.4	2.0	2.2	0.8	2.1	1.76
Parent Material	Alluvium basaltic	Alluvium	Basalt	Rhyolite alluvium	Alluvium basaltic	Alluvium basaltic

30 cm x 60 cm sampling frame. Thirty samples at each site were recorded. Shrub cover using a line-intercept approach was also determined along each 30 m transect. Herbage production of understory species was measured the following year utilizing the same sampling scheme as that used for plant frequency analysis. Plants were clipped and oven dried at 60°C for 48 hours.

Soils were classified according to Soil Conservation Service (1975) definitions, and topographic characteristics noted at each location. Soil pH, surface texture, percent organic matter and parent material were also determined. Estimates of mean annual precipitation values for each site were taken from U.S. Department of Commerce records from the nearest weather stations and averaged during the years 1962 to 1977.

Results and Discussion

Vegetation and Soils

Graminoids were the prominent understory species in the ARTRW/FEID habitat type, with Idaho fescue the dominant bunchgrass present on all sites (Table 2). Thurber's needlegrass was found to be a frequent associate particularly on sites with sandy soil, but contributed less to understory biomass than Idaho fescue. Sandberg bluegrass and squirreltail were common members of the plant association. At the Squaw Butte and Hampton locations, scattered individuals of bluebunch wheatgrass, western wheatgrass, and junegrass were encountered, but contributed little to the understory component. Cheatgrass brome achieved maxmium expression within stands found on coarse textured soils. Although perennial forbs did not constitute a very large percentage of the understory component, pussytoes (*Antennaria dimorpha*) was ubiquitous. Annual forbs as a group tended to be clustered under shrub canopies and were less common in shrub interspaces. Canopy coverage of Wyoming big sagebrush ranged from 7 percent to 25 percent. Green rabbitbrush (*Chrysothamnus viscidiflorus*) did not appear to be an important component of the ARTRW/FEID habitat type, but did occur on sites with coarse textured soils.

Evaluation of soil characteristics within the sampled stands revealed differences in texture in relation to geographic area as soils on the Squaw Butte and Hampton sites were coarser textured than those encountered at the Baker location (Table 1). Soil textures ranged from silt loams to loamy sands. Soil pH's ranged from 6.7 to 7.4 and soils parent materials were generally derived from an alluvial source. Soil families, keying principally to xerollic durorthids, were relatively shallow, ranging from 31 cm to 76 cm to a restrictive layer.

Except for the presence of Idaho fescue and the absence of bluebunch wheatgrass, the ARTRW/FEID habitat type encountered in eastern Oregon appeared to be similar in physiognomy to the *Artemisia tridentata* ssp. *wyomingensis/Agropyron spicatum* (ARTRW/AGSP) habitat type described in Idaho (Winward 1970, Hironaka and Fosberg 1983). Both plant communities exist where annual precipitation is generally less than 30 cm and they share common understory species. Further, these two habitat types tend to be less floristically diverse than higher elevation plant communities dominated by mountain big sagebrush (*Artemisia tridentata* ssp. *vaseyana*) (Winward 1970).

Although the extent of ARTRW/FEID habitat type stands in eastern Oregon has not been assessed, it appears to occur only along the northern edge of the Great Basin in Oregon. This relationship is consistent with extensive observations of eastern Oregon rangelands. In the southeastern portion of the state, where sagebrush/grassland is the primary vegetation type, similar associations of Idaho fescue and Wyoming big sagebrush have not been located. On these sites, plant communities are like those described in Idaho, with the ARTRW/AGSP habitat type the most prevalent Wyoming big sagebrush habitat type.

Conclusions

The ARTRW/FEID habitat type encountered in eastern Oregon represents a unique plant association between Idaho fescue and Wyoming big sagebrush. Idaho fescue is probably at the edge of its tolerance range for limited moisture. Whether or not compensatory moisture relationships have enabled Idaho fescue to extend its range into Wyoming big sagebrush stands, or ecotypic development has resulted in the development of genotypes adapted to those sites has yet to be determined. Land managers may need to be extra cautious in manipulating this habitat

TABLE 2. Shrub cover, understory herbage production, relative seral stage and plant fequency for six eastern Oregon stands of the *Artemisia tridentata* ssp. *wyomingensis*/*Festuca idahoensis* habitat type.

	Stand					
	B[1]	B[2]	B[3]	S[1]	S[2]	H[1]
SHRUB CANOPY COVER						
Artemisia tridentata ssp. *wyomingensis*	19.7	13.0	13.7	13.3	25.0	6.7
Chrysothamnus viscidiflorus				6.7	0.7	4.3
HERBAGE PRODUCTION (1981) kg/ha	304	178	676	393	418	320
PERENNIAL GRAMINOIDS (Frequency)						
Agropyron smithii				3.3		3.3
Agropyron spicatum					10.0	
Carex sp.				30.0		3.3
Festuca idahoensis	36.7	16.7	100.0	23.3	53.3	56.7
Koeleria cristata					36.7	6.7
Poa sandbergii	96.7	96.7	80.0	13.3	50.0	
Sitanion hystrix	40.0	23.3	6.7	30.0	13.3	50.0
Stipa thurberiana	36.7			30.0	13.3	36.7
Stipa comata v. *comata*						13.3
ANNUAL GRAMINOIDS						
Bromus tectorum		30.0	6.7	90.0	86.7	13.3
Vulpia octoflora	3.3	3.3				
PERENNIAL FORBS						
Achillea millefolium		10.0		3.3		
Allium sp.			10.0			
Antennaria dimorpha	36.7	6.7	16.7	10.0	3.3	3.3
Arabis hirsuta v. *glabrata*				10.0		
Aster scorulorum				3.3		
Astragalus curvicarpa					23.2	
Astragalus salmonensis	53.3		23.3			
Calochortus sp.				10.0		
Chaenactus douglasii				3.3	3.3	
Crepis acuminata				3.3		
Erigeron linearis		6.7				
Erigeron poliosperum	70.0		6.7			
Eriogonum heracleoides						3.3

TABLE 2. Continued.

	Stand					
	B[1]	B[2]	B[3]	S[1]	S[2]	H[1]
PERENNIAL FORBS (continued)						
Leptodactylon pungens						10.0
Lomatium sp.	3.3	36.7				
Lomatium rollinsii			3.3			
Lomatium triternatum				3.3		
Lupinus caudatus		*16.7*		*16.7*		
Phlox hoodii	76.7	60.0	23.3		13.3	
ANNUAL FORBS						
Alyssum alyssoides		26.7	10.0		60.0	
Collinsia parviflora		6.7	83.3	40.0	16.7	86.7
Descurainia pinnata						10.0
Epilobium paniculatum		40.0				
Eriastrum sparisflorum						3.3
Eriogonum vimineum						16.7
Gayophytum ramosissimum						13.3
Lepidium perfoliatum		33.3	3.3			
Microsteris gracilis			60.0	96.7	90.0	76.7
Plectritis macrocera	33.3	16.7				
Ranunculus testiculatus		16.7				
SHRUBS						
Artemisia tridentata ssp. *wyomingensis*	50.0	33.3	23.3	23.2	46.7	6.7
Chrysothamnus viscidiflorus				6.7	3.3	36.7

type. With Wyoming big sagebrush growing well within its ecological range and Idaho fescue at its edge, Idaho fescue may be very sensitive to heavy livestock utilization.

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Geomorphic Surfaces and Soils, Northwestern Whatcom County, Washington

Abstract

The geomorphology and soils of northwestern Whatcom County reflect a sequence of depositional and erosional events resulting from glacial and fluvial processes. Four geomorphic surfaces were identified and correlated to soil taxa. They range in age from late Holocene to late Pleistocene. The lower flood plain supports Entisols, the upper one Entisols and Mollisols, the outwash terraces Spodosols and some Alfisols, and the glacialmarine drift plains Alfisols. Radiocarbon dates of organic deposits (9,920 ± 760 to 9,300 ± 250 years B.P.) and seashells (12,090 ± 350 to 10,370 ± 300 years B.P.), topographic position, relative age, and the presence or absence of volcanic ash from Mount Mazama (6,600 years B.P.) are used to identify the surfaces.

Introduction

The geomorphology and soils of northwestern Whatcom County reflect a sequence of depositional and erosional events resulting from glacial and fluvial processes (Goldin in press). Each episode of landscape development can be delineated as a geomorphic surface (Parsons *et al.* 1970). The soils associated with a particular surface are differentiated primarily by contrasts in drainage and the texture of the parent material.

The purpose of this paper is to examine the interrelationships among soils, geomorphology, and time.

Methods

Geomorphic surfaces for about 80,000 ha were mapped on 1:63,360 aerial photographs (Figure 1). Sequential field relationships among surfaces, elevations, and photo interpretation of tonal patterns were used to map the surfaces. The soils were studied according to standard procedures and terminology (Soil Conservation Service 1981, Soil Survey Staff 1975). Twelve of the 13 soils on the outwash terraces, all 4 on the glacialmarine drift plains, and the 2 soils on the delta have their series type locations in the study area. All of the soils in the study area are established series.

Results

Soils

None of the soils have significant accumulations of translocated organics, clay, sodium, or carbonates in the subsoil. The annual precipitation of 750 to 1500 mm has leached most of the soluble materials below the zone of observation. Whatcom soils have some carbonates. These are present in the marine sediments and are difficult to leach because of the slow permeability of the soils. They also have some argillans.

The structure is weak in most of the soils. The strongest structure in the subsoil occurs in soils with high clay contents (Bellingham soils) and in the Spodosols with iron cementation (Edmonds and Woodlyn soils).

The major distinctive horizons in the study area are the E and upper Bsm horizons in the poorly drained Spodosols and the Ap and Bg horizons on the cultivated poorly drained soils. The well drained and moderately well drained soils on the two older surfaces have silt pellets and cracked coatings within the B horizon.

Geomorphic Surfaces

Surface 1 This surface is the lower, active flood plain of the Nooksack River and is the depositional and erosional environment of the river channels and associated point bars and channel fillings (Figure 2). The surface is generally underlain by coarse alluvium and is subject to annual flooding. The deposits are pebbles, sand, and silt. The landscape configuration is not stable and changes rapidly as a result of the cutting of new channels, abandonment of older channels, and downstream movement of alluvial deposits.

The age of the surface is late Holocene. Elevation ranges from sea level to 50 m. Slopes are 0 to 3 percent. The principal soils on this surface are the Pilchuck soils, which are very deep, somewhat excessively drained, and composed of unweathered sand. Pilchuck soils have no

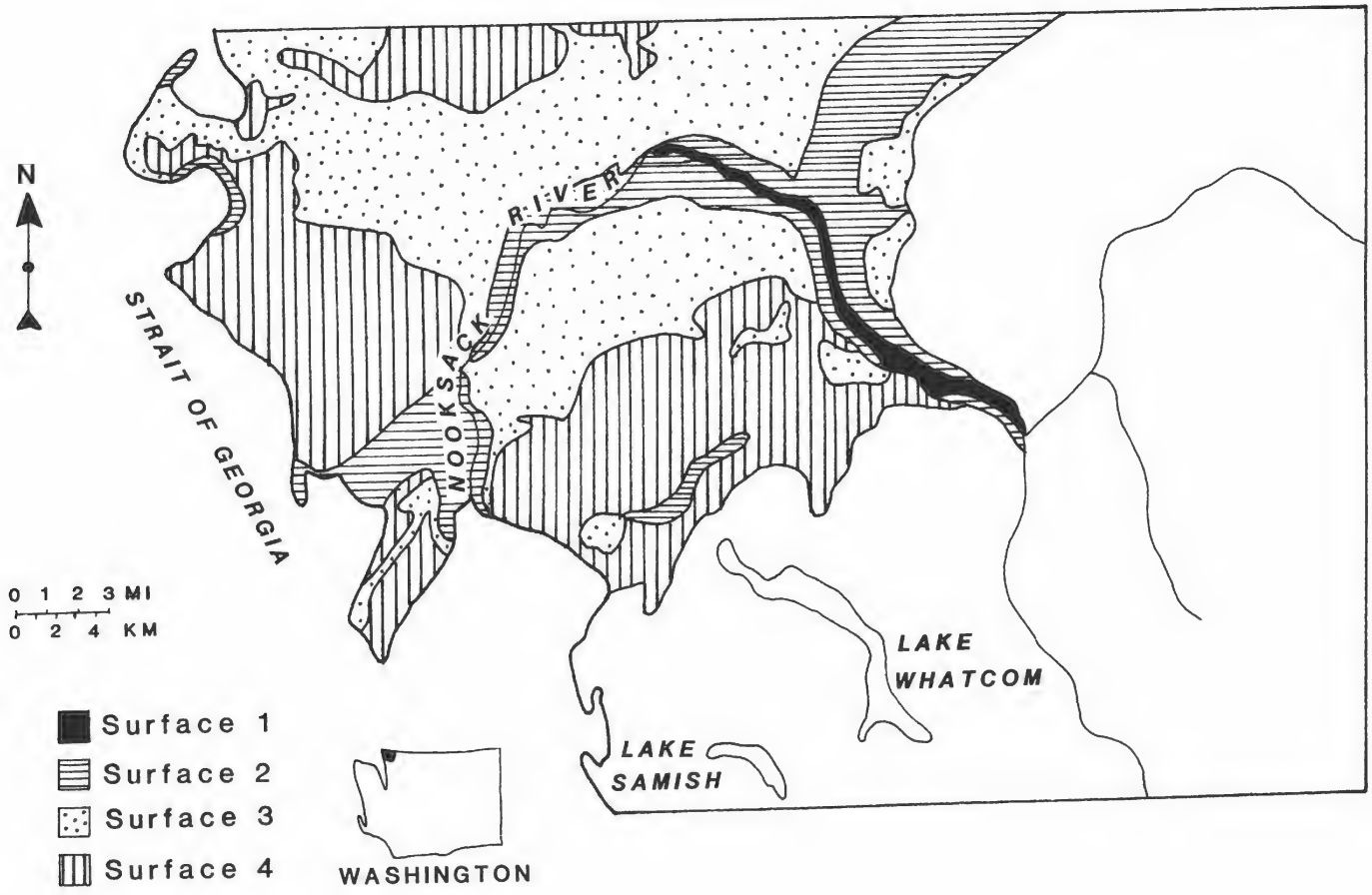

Figure 1. Map of the geomorphic surfaces in northwestern Whatcom County, Washington.

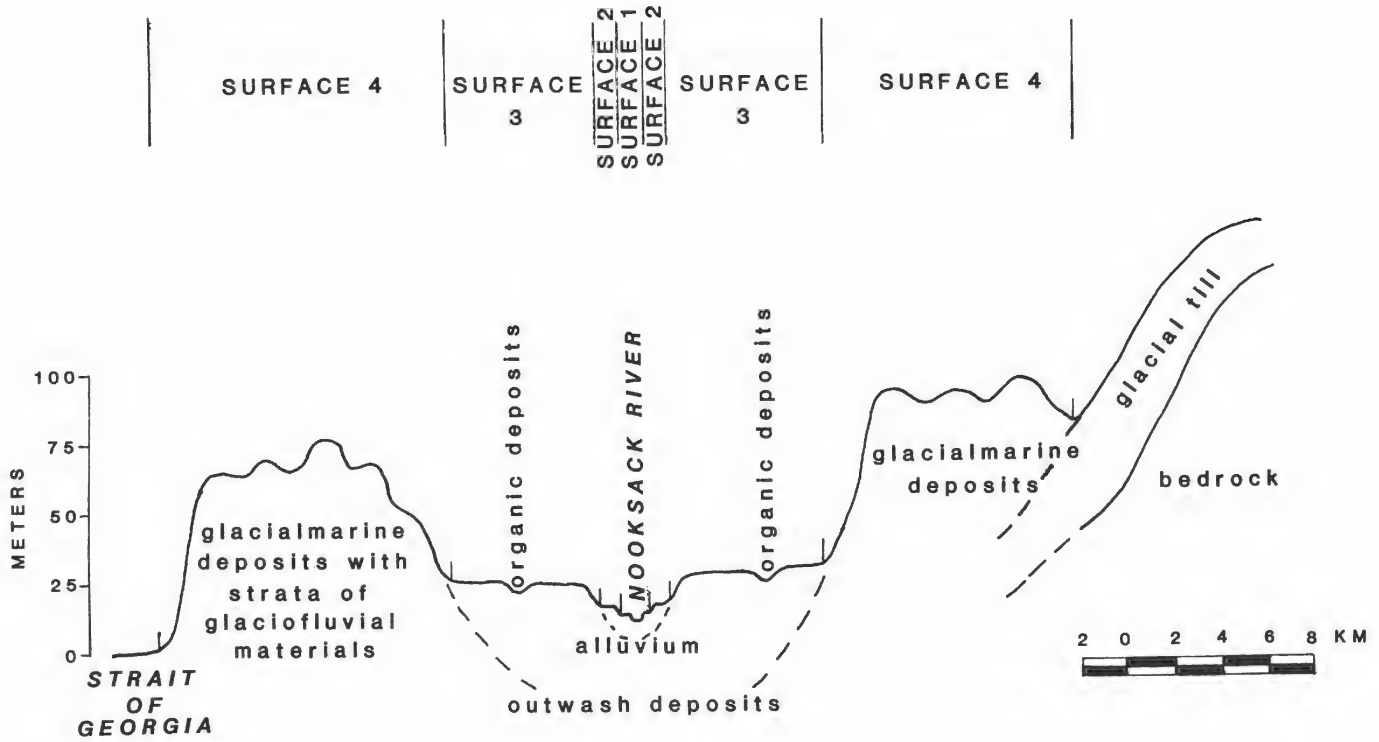

Figure 2. Idealized topographic profile and geomorphic surfaces in northwestern Whatcom County, Washington.

diagnostic features other than an ochric epipedon (Soil Survey Staff 1975) and are Dystric Xeropsamments (Soil Survey Staff 1984). Riverwash is also a major component of this surface.

Surface 2 This surface is the higher of the two flood plains and includes the levees, the valley flat, and the modern delta of the Nooksack River. The deposits generally are stratified sand, silt, and clay. The alluvium is derived from a variety of rocks, but is dominated by andesite and metasedimentary materials (Easterbrook 1971). Alluvial fans and coastal beach deposits are included in this surface. Some organic deposits occur in former quiet backwater areas. Elevation ranges from sea level to 60 m. Slope is dominantly 0 to 2 percent but is as steep as 8 percent on alluvial fans.

Deposition started on this surface after the Sumas Stade of the Fraser Glaciation about 10,000 years B.P. No properties associated with volcanic ash are evident in the soils. Since the ash in western Whatcom County originates from Mount Mazama (Easterbrook 1971, Lidstrom 1972), the lack of Mazama ash within this surface indicates that it is younger than 6,600 years. This surface is probably middle to late Holocene.

Soils of this surface have few prominent morphological features; they are differentiated mainly by the texture of the parent material. Most have a fluctuating water table, as indicated by the mottling in the underlying material within a depth of 0.5 m.

The soils of the levees are very deep, nearly level, and have a mollic epipedon. They are the well drained Puyallup and the moderately well drained Mt. Vernon soils, which are Fluventic and Fluvaquentic Haploxerolls, respectively.

The soils of the delta are very deep, very poorly drained, and contain sulfidic materials. The principal soils are the Eliza and Tacoma soils (Sulfic Fluvaquents), which are subject to salt intrusion as a result of their proximity to the sea.

The soils of the valley flat are very deep and poorly drained Aeric Fluvaquents, represented by the Briscot and Oridia series. These soils and those on the delta have no diagnostic horizon other than an ochric epipedon.

Surface 3 This surface is dominantly outwash terraces, but also includes proglacial lacustrine terraces. The outwash terraces consist of sand with various amounts of gravel. Depressions in the outwash terraces, both channels and kettles, commonly contain organic deposits. Lake beds and low-relief, abandoned channels filled with organic materials are typical of surfaces of this age in western Oregon (Parsons *et al.* 1970) and southcentral Washington (Goldin and Parsons 1983), although these latter surfaces are not developed in glacial materials. The glaciolacustrine deposits consist of silt and clay, which are distinctly varved in some areas. A thin layer of aeolian materials, which include volcanic ash, mantles this surface (Armstrong 1981).

Surface 3 is the oldest surface related to the present drainage system. The ancient drainage pattern parallels that of the modern flood plain indicating that the Nooksack River is a remnant of the preexisting glacial drainage system. The competence of the proglacial streams was greater than that of the modern Nooksack River and the valley was broader. This is indicated by the deposits, which are coarser and more extensive than the modern alluvial materials. The texture of the soils reflects this difference.

The highly competent glacial streams deposited materials high in rock fragment content, in which the Kickerville, Barnhardt, and Clipper soils formed. Slower moving waters deposited stratified sands and some silts low in rock fragment content; these sediments were later reworked by wind. The Lynnwood, Lynden, Laxton, Tromp, Hale, Edmonds, and Woodlyn soils formed in these deposits. The admixture of silty aeolian deposits and organic matter into these soils has markedly increased their fertility (Goldin 1983). Elevation ranges from 15 to 100 m, and slopes range from 0 to 15 percent.

Carbon 14 dates obtained from the base of the organic deposits range from 9,920 ± 760 to 9,300 ± 250 years B.P. (Easterbrook 1971, Armstrong 1981). The outwash and glaciolacustrine deposits are slightly older than these dates, and the surface is slightly younger, corresponding to late Pleistocene. Deposition occurred during the Sumas Stade of the Fraser Glaciation. The organic soils commonly contain strata of volcanic ash (Rigg 1958) from the eruption of Mount Mazama as do similar aged soils reported from other areas of the Pacific Northwest (Balster and Parsons 1968, Goldin and Parsons 1983).

The soils of the outwash terraces are very deep to shallow, somewhat excessively drained to poorly drained, and nearly level to gently sloping. The lower part of the profile is sandy and

contains 0 to 60 percent coarse fragments. The upper part of the profile of most of these soils formed in aeolian deposits that include volcanic ash. Each of the soils on this surface has a spodic horizon. The principal soils are the well drained Lynden and Kickerville soils, which are Typic Haplorthods, and the moderately well drained Tromp and somewhat poorly drained Hale soils, which are both Aquic Haplorthods. The poorly drained Edmonds and Woodlyn soils are Typic Sideraquods. A continuous hardpan (ortstein layer) strongly cemented with iron has developed within a depth of 0.5 m in Woodlyn soils. This layer, which formed from the deposition of iron at the water table, is fragmented in the Edmonds soils.

Upon glacial recession, meltwater flow decreased. Abandoned outwash channels and, to a lesser extent, kettles and other depressions in the flood plains supported wetland plants, such as rushes, sedges, and some woody plants in the stagnant water (Rigg 1958). When the plant material died, it accumulated and became the parent material for the very deep, very poorly drained, nearly level Pangborn (Typic Medisaprists), Shalcar, and Fishtrap soils (Terric Medisaprists).

The soils of the glaciolacustrine terraces are very deep, somewhat poorly drained and poorly drained, and nearly level to gently sloping on ridge-swale topography. Skipopa soils (Aqualfic Haplorthods) on the ridges have a silty aeolian mantle over a clayey substratum. They have a spodic horizon and an argillic horizon. Bellingham soils (Typic Argiaquolls) in the swales have a mollic epipedon and an argillic horizon and are clayey throughout the control section.

Surface 4 This surface consists of glacialmarine deposits with an aeolian mantle that includes volcanic ash (Pevear *et al.* 1984). The rolling topography reflects the deposition from melting ice of debris that ranges in size from clay to boulders. In the western part of the survey area, poorly sorted glaciofluvial materials up to 60 cm thick lie between the aeolian mantle and the glacialmarine deposits. Elevation ranges from 20 to 120 m, and slopes range from 0 to 60 percent.

The age of this surface has been determined from the dating of fossil shells in the glacialmarine deposits. Dates range from 12,090 ± 350 to 10,370 ± 300 years B.P. (Easterbrook 1971, Armstrong 1981). The material was deposited in the late Pleistocene during the Everson Interstade of the Fraser Glaciation prior to the inception of the Sumas Stade. Dates from marine terraces and peat bogs overlying these deposits show that the area was rapidly uplifted isostatically during this time (Easterbrook 1963).

On glacialmarine drift plains not overlaid by the glaciofluvial materials, the soils are very deep, moderately well drained and poorly drained, and nearly level to steep. The Whatcom soils (Aqualfic Haplorthods) have a spodic horizon and an argillic horizon and occupy the higher and steeper parts of the landscape. The Labounty soils (Typic Umbraqualfs) have an umbric epipedon and an argillic horizon and occupy the lower parts.

The soils with interbedded glaciofluvial deposits are very deep, moderately well drained and poorly drained, and nearly level to gently sloping. The Birchbay (Typic Haplorthods) and Whitehorn soils (Typic Umbraqualfs) are similar in morphology and landscape position to the Whatcom and Labounty soils, respectively, but have coarser textures in the upper part of the substratum.

Although clay films in the Whatcom, Labounty, Skipopa, Bellingham, and Whitehorn soils are uncommon, micromorphological evidence in the form of argillans indicates the development of an argillic horizon. The classification of the spodic horizon on surfaces 3 and 4 is based on the discovery by USDA's National Soil Survey Laboratory of silt-sized pellets and some cracked coatings in the B horizon. The soils do not meet the chemical criteria for a spodic horizon.

Summary

The soils of northwestern Whatcom County, Washington show increasing development on each successively older geomorphic surface. The diagnostic horizons requiring the most time to form (argillic horizon and spodic horizon) are on the oldest surfaces (surfaces 3 and 4). The horizon requiring the least time to form (ochric epipedon) is on the youngest surface. The argillic horizon has formed only on the finer textured soils on these surfaces. The horizon requiring intermediate time (mollic epipedon) is on the middle surface (surface 2).

All soils within a geomorphic surface need not exhibit the same degree of profile development

since they vary in landscape position or parent material. Examples are the outwash and glaciolacustrine soils on surface 3 and the levee and valley flat soils on surface 2. Geomorphic mapping at a larger scale would help to make these separations. Soil-geomorphic surface relationships also help to estimate the time for the development of a horizon, although it should be understood that other factors besides time are responsible for horizon formation. In this study, the spodic horizon forms in about 9,300 to 9,900 years and the argillic horizon in about 10,000 to 12,000 years.

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The September 24, 1984 issue of *Current Contents/Agriculture, Biology and the Environmental Sciences* named Rexford Daubenmire's article, "A canopy-coverage method of vegetational analysis," as a "Citation Classic." Daubenmire's article, which appeared on pages 43-64 of *Northwest Science* 33 (1959), has been cited over 185 times, more than any other paper published in this journal. According to Current Contents, "The relative impact of each classic can be seen by considering that the average 1973 article published in an *SCI*-covered source journal was cited approximately ten times between 1973 and 1982."

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On the Holocene History of *Ursus* in Eastern Washington

Abstract

The Holocene archaeological record for *Ursus* in eastern Washington indicates that (1) *U. americanus* occupied a range during the Holocene similar to its historical range, and (2) *U. arctos* occupied a larger range than that historically documented. Frequencies of ursid remains appear to remain stable throughout the Holocene in spite of major changes in environment and human hunting practices.

Introduction

When Walter Dalquest published his study on the mammals of Washington in 1948, archaeology and paleontology were just beginning to become major research endeavors in the state (Sprague 1973). Today a body of paleomammalogical data is available as a result of those research endeavors over the past 35 years. I summarize those data for the genus *Ursus,* and give some paleoecological and archaeological interpretations for Washington east of the crest of the Cascade Range. This area is physiographically diverse (Franklin and Dyrness 1973), and includes the Columbia Plateau, the eastern flanks of the Cascade Range, the Okanogan Highlands, the western edge of the Selkirk Mountains, and the northern portion of the Blue Mountains.

Hall (1981) recorded 93 extant endemic mammalian species, representing 58 genera, in this study area. The zoogeographic history of these taxa has been dynamic over the past 20,000 years, and several other taxa became locally extinct. Archaeological records of taxa tend to confirm the speculative zoogeographic history outlined by Dalquest (1948). At present, 43 species representing 35 genera have been identified in Holocene archaeological sites in eastern Washington (Lyman and Livingston 1983).

Methods

Data for this study were derived from published and unpublished archaeological and paleontological reports. Because the taphonomic history of a bone assemblage is difficult to ascertain, the extent to which a sample of faunal remains resembles the original fauna from which it derived cannot be determined (Grayson 1981, King and Graham 1981). It is reasonable to assume, however, that taxa represented in an archaeological faunal assemblage lived in the general area of the site of recovery. Multiple samples of faunal remains from numerous regional sites are required to demonstrate that a taxon was absent (Grayson 1981). I have assumed that the present ecological requirements of the taxa discussed are the same as that in the past. I also assume that palynological data reflect prehistoric environmental conditions.

The available palynological data indicate that prior to about 9500 yr B.P. environments tended to be cooler than at present, with dry conditions in the southern two thirds and humid conditions in the northern one third of eastern Washington. The environment then tended to become warmer and/or drier, with a brief moist interval about 8000 to 8500 yr B.P. in some higher elevations. About 4500 yr B.P. environments shifted to cooler and moister conditions than found today. Subsequent to 2500 yr B.P., environments in all parts of eastern Washington became much like modern environments. There is limited evidence of a drier episode between 1500 and 500 yr B.P. in more arid parts of eastern Washington (see Mehringer in press, and references therein).

Results

Ursus americanus

Hall (1981:950) indicated that *U. americanus* was historically ubiquitous in the state, but Dalquest (1948:175) suggested a more limited distribution (Figure 1). Most recently, Pelton (1982:504) proposed that "the primitive range of *U. americanus* covered the forested areas of North America" and excluded the arid Columbia Plateau of eastern Washington from its range.

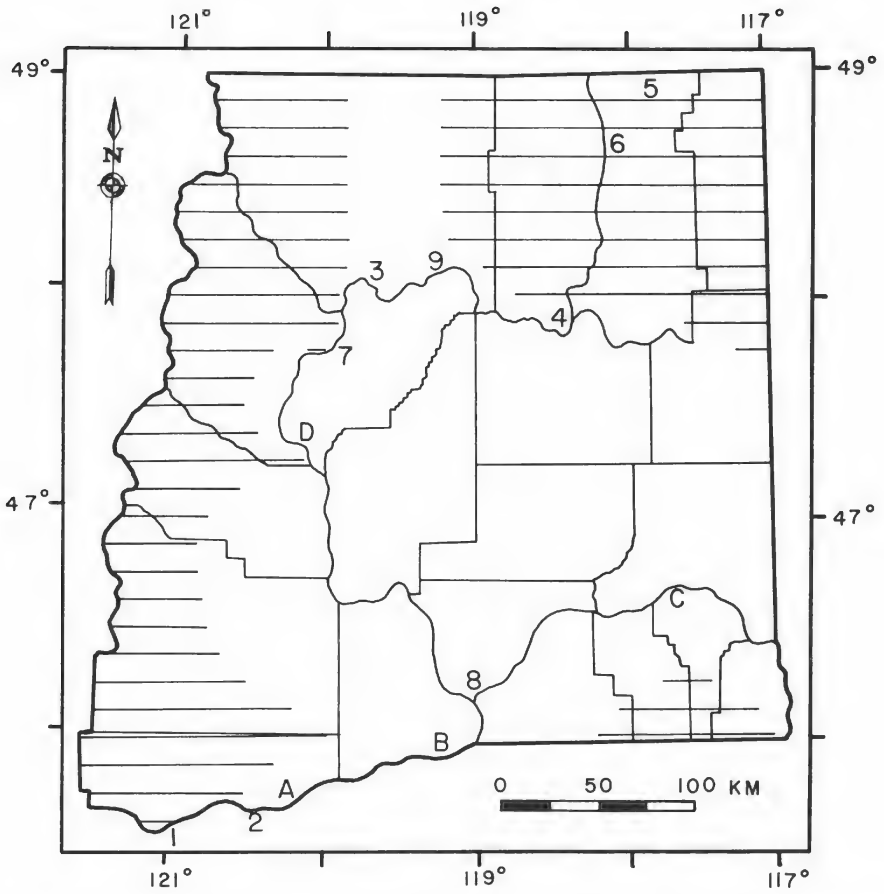

Figure 1. Holocene archaeological and historically documented distributions of *Ursus* sp. and *U. americanus* in eastern Washington. The horizontally cross-hatched area is the historic distribution of *U. americanus* (Dalquest 1948). Numbers indicate recovery sites of *U. americanus* remains, and letters indicate recovery sites of *Ursus* sp.

No ursid specimens have been reported from any of a dozen archaeological sites that have been excavated in the arid Columbia Plateau. The number of specimens from each of these sites tends to be small (range is 5 to 3622; $\overline{X} = 557$), therefore it is possible that future work will recover *Ursus* remains from this area. It is well documented that large samples are required to detect the presence of rare taxa (*e.g.*, Wolff 1975). At present I can only conclude that ursids were rare, if present at all, in the arid Columbia Plateau.

The available Holocene data conform most closely to the distribution indicated by Pelton (1982). Specimens of bones and teeth recovered from archaeological sites and identified as *U. americanus* have been found in eight sites that are today in forested environments (Table 1). All of these sites are in riverine locations, where trees and brush are more abundant than on contiguous uplands.

Ursus arctos

The grizzly apparently entered the contiguous 48 states during the Wisconsinan glacial episode (Kurtén and Anderson 1980:184). Craighead and Mitchell (1982:516) summarized the available North American zoogeographic data for *U. arctos*

TABLE 1. Summary of Holocene archaeological ursid data in eastern Washington. *see Figure 1. **see Figure 2.

TAXON	SITE	YEARS B.P.	NUMBER OF SPECIMENS	REFERENCE
Ursus sp.	*(A)45KLa	late Holocene?	"present"	Garth, 1952
	*(B)45BN55	late Holocene?	"present"	Garth, 1952
	*(6)45FE44	9000-4400	7	Chance and Chance, 1982
	*(C)45Ga17	2330	"present"	Schroedl, 1973
	*(D)45D0176	850	1	Lyman, 1985b
	*(9)450K258	800-600	2	Livingston, unpublished
	*(9)450K258	3500-2200	2	Livingston, unpublished
U. americanus	*(1)35WS4	mid-Holocene?	"present"	Cressman et al., 1960
	*(2)35GM9	6700-0	4	Dumond and Minor, 1983
	*(3)450K52	500	"present"	Grabert, 1968
	*(4)45FE24	late Holocene?	4	Collier et al., 1942
	*(5) 46	late Holocene?	1	Collier et al., 1942
	*(6)45FE45	6000-4400	12	Grayson, 1977
	*(6)45FE45	4400-3200	2	Grayson, 1977
	*(6)45FE45	3200-2800	2	Chance and Chance, 1982
	*(7)45D0408	1450	1	Schalk and Mierendorf, 1983
	*(8)45FR5	500	1	Olson, 1983
	*(9)450K11	5000-4400	4	Livingston, unpublished
U. arctos	**(1)45D0176	850	2	Lyman, 1985b
	**(2)45FE44	9000-4400	4	Chance and Chance, 1982
	**(3)450K11	3900-2800	1	Livingston, unpublished
	**(4)45FR50	unknown	1	Gustafson, 1972
	**(5)45GA17	2330	1	Gustafson, 1972

and noted that "it is clear that this taxon was once native to a far more extensive area of North America than it now inhabits."

While over 110 Holocene archaeological sites in eastern Washington have produced faunal remains, only 5 of these sites contained the remains of *U. arctos* (Figure 2). This suggests that *U. arctos* was either less abundant than *U. americanus* during the Holocene of eastern Washington or that *U. arctos* was pursued less often by prehistoric human hunters. Although all five sites containing the remains of *U. arctos* are located in riverine settings, four of these appear to be outside of the range historically documented for this taxon. Virtually all Indian groups living in eastern Washington during the late Holocene hunted both species of bear for meat and hides, and many of these groups afforded grizzly bear bones special ceremonial treatment. Therefore, Gustafson (1972:72) suggested that the grizzly bones from sites 45GA17 and 45FR50 "could have been carried to the sites from forested areas in the nearby mountains." The *U. arctos* bones thus far recovered are: 45FR50—phalanx; 45GA17—metacarpal; 45D0176—left mandible and M_3; 450K11—metapodial; and 45FE44—unknown. The bones of the feet might have been attached to a hide, and the mandible and tooth may have been part of a skull used in a ritual. These elements have little food value to humans (Lyman 1985a), and would not have been transported for this reason. While some of the specimens may in fact have been transported long distances (over 50 km) by people, the suggestion that grizzlies occupied a larger range prehistorically than historically tends to be confirmed by the archaeological data. Because most of the Holocene archaeological sites thus far excavated are located along the banks of the Columbia, Snake, and Okanogan Rivers, and in the most arid parts of

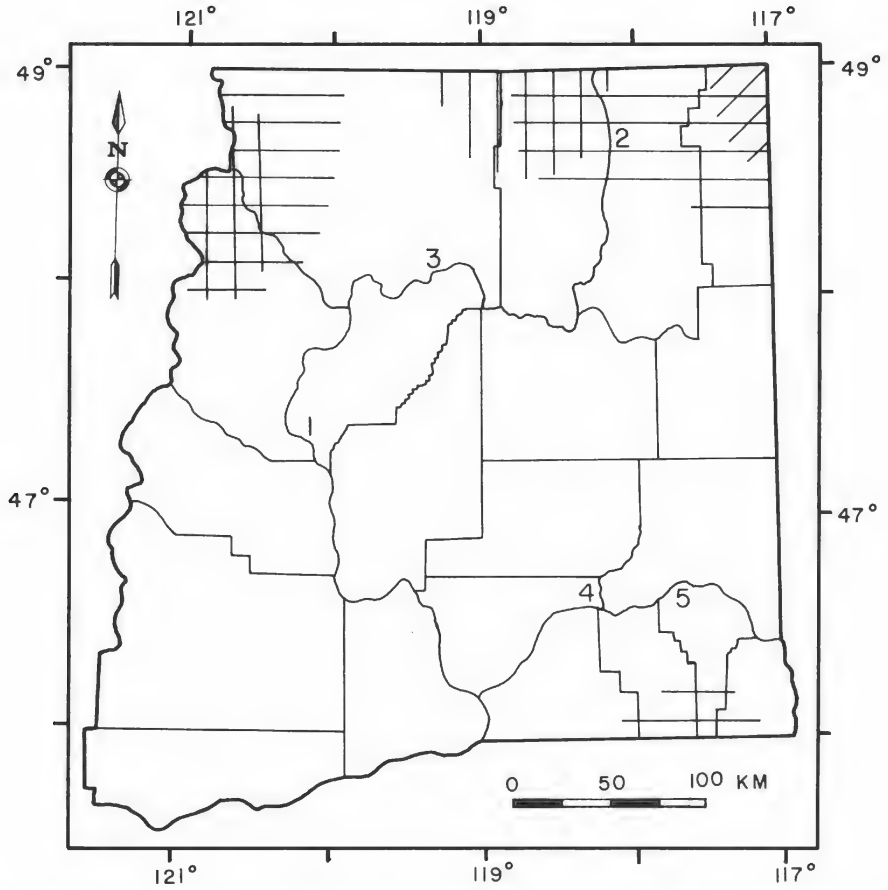

Figure 2. Holocene archaeological and historically documented distributions of *U. arctos* in eastern Washington. The horizontally cross-hatched areas (Dalquest 1948), the vertically cross-hatched areas (Layser 1978), and the diagonally cross-hatched area (Zager 1983) have all been documented for the historic period. Numbers indicate recovery sites of *U. arctos* remains.

the state (Lyman and Livingston 1983), I predict that Holocene records of *U. arctos* will eventually be found in the eastern flanks of the Cascades and in the extreme northeastern part of Washington.

Discussion

The number of *Ursus* specimens recovered ranges from one to 16 per site ($\bar{X} = 4.4$, $\sigma = 4.6$). Precise dating for some of the specimens is lacking, but all date to the last 9000 years. Did the abundance of ursids fluctuate through the Holocene? Northcott and Elsey (1971) reported that the population of hunter-killed *U. americanus* in Ontario was greatest during years with warm, dry, spring months, and was least in years with heavy autumn snowfall. The former, they suggested, may allow earlier emergence and movement of ursids as well as more hunter activity. In contrast, they suggested that early heavy snowfall would lead to premature denning when ursids are physiologically not ready to hibernate (and survive) an entire winter. If winters were milder between 8000 and 4500 yr B.P., as suggested by the palynological data, and the

intensity of ursid hunting by humans was greater, then a greater number of ursid remains is expected in the faunal record dating to this time period.

If only the ursid specimens with absolute dates prior to 4400 yr B.P. (N = 27) and after 4400 yr B.P. (N = 15) are considered, it appears that ursids may have been more abundant in the pre-4400 yr B.P. interval ($\chi^2 = 3.428$, $p < .075$). If the specimens that *may* date to the late Holocene are added (N = 20), then ursids do not appear to have been more abundant prior to 4400 yr B.P. ($\chi^2 = 1.042$, $p > .3$). If only those specimens dated to 2000 yr or less time periods are considered, the 0 to 2000 yr B.P. temporal segment has 7 specimens from 4 sites, the 2000 to 4400 yr B.P. segment has 8 specimens from 4 sites, and the 4400 to 6000 yr B.P. segment has 16 specimens from 2 sites. Any apparent decrease in ursid abundance may therefore be a function of the sites sampled. For example, 12 of the 16 specimens dated to the 4400 to 6000 yr B.P. segment come from a single site (45FE45) and may represent a single individual animal, while the minimum number of individual animals during the other time intervals is certainly at least four.

A temporally coincident decrease in the abundance of ursid remains and change from harsh to mild winters would suggest a causal relationship. Such an interpretation would, however, be difficult to substantiate because a major change in cultural adaptive strategies occurred about 4500 to 4000 yr B.P. Human occupants of eastern Washington altered their settlement-subsistence practices from following a relatively opportunistic nomadic hunting and gathering lifeway prior to 4500 yr B.P. to a semi-sedentary fishing, plant-gathering, and hunting lifeway wherein people depended more heavily on stored fish and plant resources during winter by about 4000 yr B.P. (Ames 1982, Galm *et al.* 1981, Schalk and Cleveland 1983). This change may have resulted in an altered emphasis on the hunting of ursids for subsistence.

Conclusion

There is no apparent change in ursid abundance coincident with palynologically documented environmental change, perhaps because of one or both of two factors: (1) changing human subsistence practices, and/or (2) the ursid remains considered here are not representative of the prehistoric ursid populations. It is nonetheless significant that the geographic distribution of the remains confirm the zoogeographic histories postulated for ursids in eastern Washington.

Acknowledgments

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Energy Dispersive X-Ray Fluorescence Analysis of Obsidian From Dog Hill and Burns Butte, Oregon

Abstract

Non-destructive energy dispersive x-ray fluorescence analyses were performed on rhyolitic volcanic glasses (obsidian) from Dog Hill and Burns Butte, Oregon. Sixteen trace and rare earth element concentrations were determined in parts per million (ppm) for each source, showing that these two obsidian sources are quite distinctive geochemically despite their close proximity to one another. In addition to demonstrating geochemical differences between sources, the results of the present study show that archaeological artifacts from east-central Oregon can be matched to these sources on the basis of quantitative measurements of trace element compositions.

Introduction

Over the past few years, archaeologists increasingly have employed techniques derived from the physical sciences to assist in detecting patterning in archaeological residues. In western North America considerable interest has accrued to obsidian studies, because obsidian can be used to establish chronological sequences through obsidian hydration dating (*cf.* Friedman and Long 1976, Michels and Tsong 1980), and because the geochemical composition of volcanic glass makes it possible to determine the parent geological source of materials used to manufacture prehistoric tools. Once the parent sources of obsidian have been characterized geochemically, artifacts from archaeological sites can be analyzed and assigned to their probable geologic source on the basis of similarities in trace and rare earth element composition. This step completed, it is then possible to attempt reconstructing prehistoric distribution (or exchange) routes and to investigate changes or continuities in direction and intensity using different categories of tools to monitor different kinds of prehistoric activities (*e.g.* Hughes 1986b, Hughes and Bettinger 1984).

Despite the large number of obsidian source deposits in Oregon, comparatively little research on prehistoric obsidian trade has been conducted in the state. This dearth of research has not occurred because of lack of interest by prehistorians, but rather because there has been, until recently, rather little published on the actual trace element composition of volcanic glasses. In short, it would be premature to inaugurate broad studies of obsidian artifacts from archaeological sites without first compiling a quantitative data base on obsidian source compositions to which the prehistoric objects can be compared. Although trace and rare earth concentration values have been published for some sources (*e.g.* Jack and Carmichael 1969, Laidley and McKay 1971, Higgins 1973, Hughes 1986b, Nelson 1984[2]), these data represent only a fraction of the total resource base. The immediate goals of this study are to present quantitative trace and rare earth element measurements on obsidian from Dog Hill and Burns Butte and, more generally, to contribute to the establishment of a geochemical data base for Oregon volcanic glasses that can be used in the service of prehistory.

One additional obstacle for archaeological research has been that previous quantitative measurements of Oregon obsidians, with one exception (Hughes 1986b), have been derived from analyses requiring crushing and powdering of some portion of the sample. This, of course, is undesirable from an archaeological perspective because of the importance of conserving unique and non-replaceable prehistoric artifacts. The non-destructive x-ray fluorescence technique employed in the present study avoids this drawback, since it is capable of generating quantitative estimates of trace and rare earth element com-

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[2]The marked disagreement between trace element concentration values for Nelson's (1984:53, source #57) "Burns" source and those generated here for Burns Butte (see Table 2) suggests that Nelson's sample was not collected from Burns Butte, but from a different locality in the vicinity of Burns.

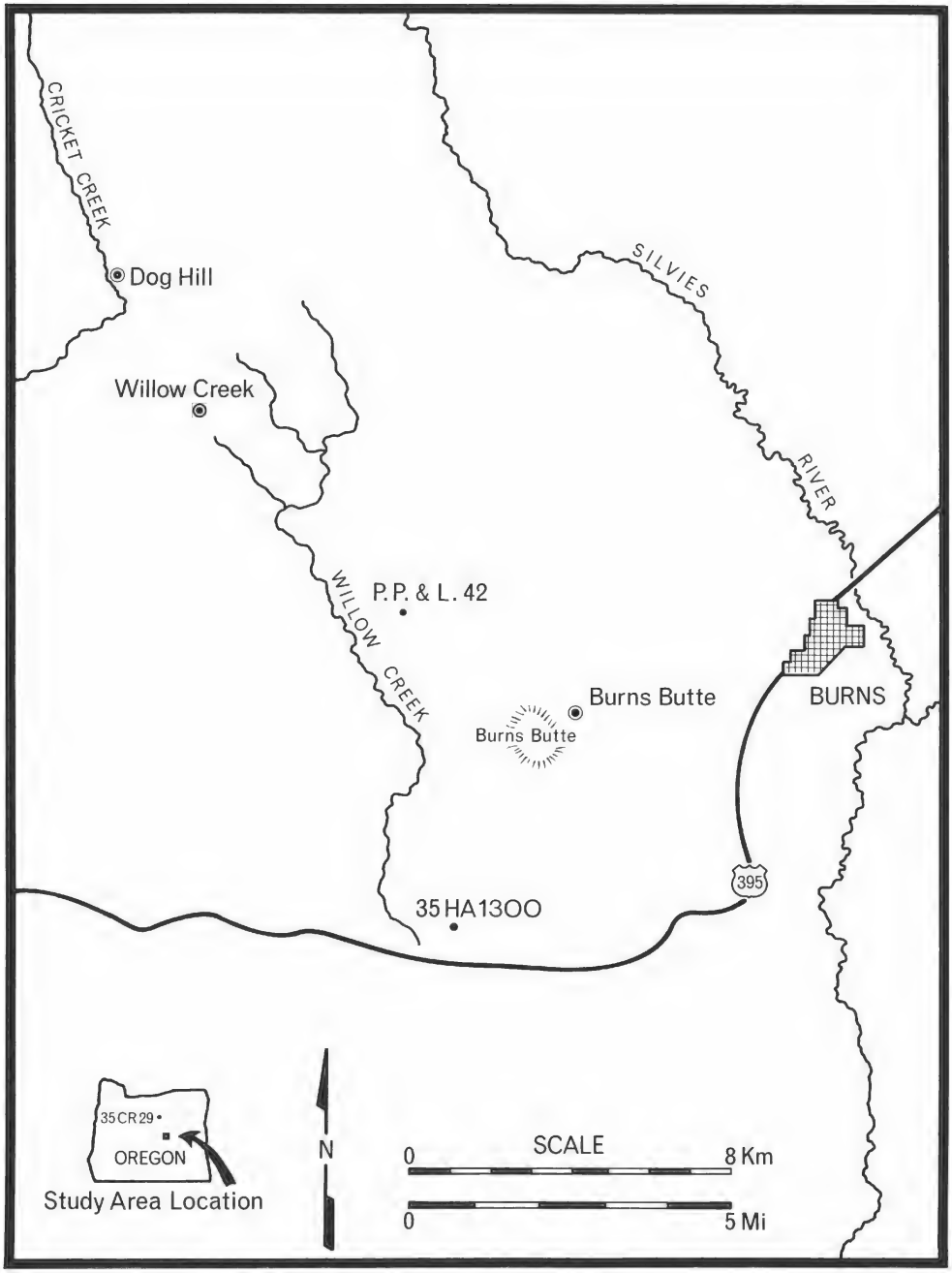

Figure 1. Map of east-central Oregon showing the locations of obsidian sources (dots within circles) and archaeological sites (dots) discussed in the text.

position that compare favorably to those determined using more time-consuming, destructive methods (*cf.* Hughes 1984, 1986a, 1986b; Nelson 1984). Once the elemental geochemistry of existing glasses is determined, it will be possible to employ these data in the study of prehistoric obsidian trade in central Oregon and adjacent areas.

The Setting

The Dog Hill obsidian source is located in the southeastern portion of the Snow Mountain Ranger District, Ochoco National Forest, Harney County, Oregon (see Figure 1). The source occupies portions of T22S, R29E, NW1/4 of Section 17 with smaller portions in the E1/2 of NE1/4 of Section 18 and the SE1/4 of the SE1/4 of Section 7 as depicted on the U.S.G.S. Burns 3 NE, 7.5 minute quadrangle, 1978 (W.B.M.). As recorded by U.S. Forest Service personnel, the source and associated prehistoric quarrying debris covered more than 200 acres on both sides of Cricket Creek, located west of the Silvies River. Samples from Dog Hill occurred locally as cobbles and nodules ranging from 20 cm to ca. 1-2 cm in diameter; these were collected systematically from three discrete zones where obsidian quarrying debris was abundant (see below).

Burns Butte has been known for some time (*e.g.* Gail 1966, Ericson 1981:182) as a source for high-quality volcanic glass (see Figure 1). Unlike the sampling procedure employed at Dog Hill, samples from Burns Butte were collected only from one restricted area in T23S, R30E, NW 1/4 of NW 1/4 of Section 21 as depicted on the U.S.G.S. Burns, Oregon, 15 minute series quadrangle, 1960 (W.B.M.). Burns Butte obsidian cobbles were larger than those observed at Dog Hill; some of these ranged up to ca. 30 cm. in diameter.

Methods

Analyses were conducted on 30 unmodified flakes (n = 15 from each source) cleaved from obsidian nodules. After flakes were detached from cobbles with a tungsten carbide mallet they were rinsed in distilled water to remove surface contaminants that might affect the analysis, catalogued, secured in position in the 20-position rotating automatic sample changer tray, and analyzed. Other than this, no sample preparation was required.

Laboratory investigations were conducted by the author at the Department of Geology and Geophysics, University of California, Berkeley, on a Spectrace 440 (United Scientific Corporation) energy dispersive x-ray fluorescence machine equipped with a Tracor Northern 1221 100 mHz analog to digital converter, a Tracor Northern 2000 computer based analyzer with a LSI-11 microcomputer with 24k word capacity, and a Si(Li) solid state detector with 142 eV resolution (FWHM) at 5.9 keV in a 30 mm^2 area. Trace element analyses in the 5-25 keV region of the energy spectrum were conducted using a Rh x-ray tube operated at 30.0 kV, .40 mA pulsed with a .04 mm Rh primary beam filter; analyses in the 20-60 keV region were made using an Am^{241} 100 mCi radio-isotope (Hughes 1986b). Ni (Kα), Cu (Kα), Zn (Kα), Ga (Kα), Pb (Lβ), Th (Lα), Rb (Kα), Y(Kα), Zr (Kα), and Nb (Kα) analytical lines were excited by the Rh x-ray tube, while Ba (Kα), La (Kα), Ce (Kα), Pr(Kα), and Nd(Kα) lines were excited by the Am^{241} source. All analyses were conducted at 200 deadtime corrected seconds (livetime). Following excitation, the contribution of overlapping Kα, K β, and L lines was subtracted (stripped) from the peaks of interest, yielding the "fingerprints" that appear in Figure 2 (*cf.* Hampel 1984). Background-subtracted net peak intensities were compared and ratioed to the Rh Kα (Franzini, Leoni, and Saitta 1976) and the Am^{241} peak continua, than converted to parts per million using a linear least squares fitting routine (Schamber 1977, McCarthy and Schamber 1981, Bice 1980:421-422).

Results

The overall accuracy of the x-ray fluorescence system is illustrated in Table 1. This table shows that most of the quantitative trace and rare earth elemental measurements generated from the present study are in close agreement with recommended values for U.S. Geological Survey international rock standards. Pr, Cu, and Ni are not measured well by non-destructive x-ray fluorescence, because concentrations for these elements in obsidians often fall below the minimum limits of detection (Vane 1977) at 200 seconds livetime.

Coefficients of variation computed from sample means and standard deviations show that these measurements vary across elements (see

TABLE 1. X-ray fluorescence determinations for trace and rare earth element concentrations in three U.S. Geological Survey standard rocks compared to recommended values. All values in parts per million. ±, counting error uncertainty at 200 seconds livetime (Schamber 1977:249).

U.S. Geological Survey Standard	Elements Th	Pb	Nd	Pr	Ce	La	Ba	Nb
W-1 (Flanagan 1976)	2.4	7.8	15.0	3.4	23.0	9.8	160.0	9.5
W-1 (This Study)	0.0 ±0.0	10.0 ±1.9	22.9 ±5.4	9.1 ±5.0	24.7 ±4.5	11.8 ±3.9	152.0 ±7.6	12.3 ±2.2
GSP-1 (Flanagan 1976)	104.0	51.3	188.0	50.0	394.0	191.0	1300.0	29.9
GSP-1 (This Study)	99.9 ±5.0	51.5 ±2.3	170.7 ±11.2	47.9 ±9.4	401.5 ±12.3	181.2 ±9.7	1237.9 ±22.2	28.7 ±2.0
G-2 (Flanagan 1976)	24.2	31.2	60.0	19.0	150.0	96.0	1870.0	13.5
G-2 (This Study)	22.3 ±3.9	34.9 ±2.1	53.7 ±10.3	14.2 ±9.3	150.1 ±9.5	78.5 ±8.2	1884.3 ±28.8	20.0 ±2.0

U.S. Geological Survey Standard	Elements Zr	Y	Sr	Rb	Ga	Zn	Cu	Ni
W-1 (Flanagan 1976)	105.0	25.0	190.0	21.0	16.0	86.0	110.0	76.0
W-1 (This Study)	107.6 ±3.1	24.1 ±2.7	187.8 ±3.7	20.9 ±2.0	16.2 ±2.8	88.9 ±6.7	111.4 ±6.7	86.9 ±8.8
GSP-1 (Flanagan 1976)	500.0	30.4	233.0	254.0	22.0	98.0	33.3	12.5
GSP-1 (This Study)	517.5 ±4.7	30.7 ±2.7	232.4 ±3.5	260.0 ±3.7	24.9 ±2.9	115.4 ±7.4	37.5 ±4.9	17.1 ±7.6
G-2 (Flanagan 1976)	300.0	12.0	479.0	168.0	22.9	85.0	11.7	5.1
G-2 (This Study)	310.5 ±3.9	14.5 ±2.5	496.3 ±4.9	178.0 ±3.2	22.2 ±2.6	97.2 ±7.0	10.6 ±3.9	10.6 ±7.1

Table 2). Th and Sr measurements, for example, are more variable than Pb, Nd, Ce, La, Ba, Nb, Zr, Y, Rb, Ga, and Zn, suggesting that they may not be as useful as the latter elements in distinguishing between obsidian sources (Hughes 1982:176, 1984). However, high "apparent" measurement error (relatively high CV% values) will be registered when the absolute concentration for an element approaches its minimum limits of detection (*e.g.* Sr concentrations in Dog Hill obsidian), and when "true" intersource elemental variability exists. In short, both instrumental measurement limitations and inherent geochemical variability may be represented in CV% values (Hughes 1986a).

As discussed above, collections were made from three different areas of the Dog Hill quarry where different surface densities of artifacts and obsidian nodules were observed. Specimens from these three areas were catalogued separately; source standards from the north collection zone have "Z2N-" catalogue prefixes, those collected from the southern area of the quarry have "Z2S-" prefixes, while samples collected from the eastern area of the site are specified by "Z3-" catalogue prefixes (Table 3). To investigate the possibility that these three collection areas contained obsidians of different geochemical composition, the nine best measured elements (Rb, Sr, Y, Zr, Nb, Ba, La, Ce, and Zn) were grouped by collection area and a one-way analysis of variance (Blalock 1972:317-334, Hays 1973:457-491) was performed on these three geographic categories (Table 4). Since the F-ratios determined for all nine elements show no significant departure from that expected by

TABLE 2. Means ($\bar{X}$), sample standard deviations (S.D.) and coefficients of variation (CV%) for 16 trace and rare earth element measurements on obsidian samples from Dog Hill and Burns Butte, Oregon. Means and standard deviations expressed in parts per million.

Element		Dog Hill Quarry (n=15)	Burns Butte (n=15)
Th	$\bar{X}$ =	5.14	6.22
	S.D. =	6.58	6.17
	CV%	128.02	99.20
Pb	$\bar{X}$ =	41.65	23.55
	S.D. =	3.09	1.33
	CV% =	7.42	5.65
Nd	$\bar{X}$ =	65.75	28.95
	S.D. =	7.39	4.40
	CV%	11.24	15.20
Pr	$\bar{X}$ =	20.11	10.25
	S.D. =	7.32	7.42
	CV% =	36.40	72.39
Ce	$\bar{X}$ =	145.01	79.09
	S.D. =	7.81	7.84
	CV%	5.39	9.91
La	$\bar{X}$ =	67.85	43.13
	S.D. =	4.69	6.46
	CV%	6.91	14.98
Ba	$\bar{X}$ =	47.25	604.62
	S.D. =	7.35	44.42
	CV%	15.56	7.35
Nb	$\bar{X}$ =	34.74	24.13
	S.D. =	4.75	2.52
	CV% =	13.67	10.44
Zr	$\bar{X}$ =	579.80	233.58
	S.D. =	48.88	20.22
	CV% =	8.43	8.66
Y	$\bar{X}$ =	89.85	41.53
	S.D. =	8.29	4.43
	CV% =	9.23	10.67
Sr	$\bar{X}$ =	2.86	25.87
	S.D. =	2.02	2.24
	CV% =	70.63	8.66
Rb	$\bar{X}$ =	116.42	119.47
	S.D. =	7.57	7.34
	CV% =	6.50	6.14
Ga	$\bar{X}$ =	21.90	17.15
	S.D. =	3.30	1.82
	CV% =	15.07	10.61
Zn	$\bar{X}$ =	159.56	29.11
	S.D. =	14.20	5.15
	CV% =	8.90	17.69
Cu	$\bar{X}$ =	5.59	9.12
	S.D. =	10.08	7.97
	CV% =	180.32	87.39
Ni	$\bar{X}$ =	2.18	0.29
	S.D. =	3.29	0.57
	CV% =	150.92	196.55

TABLE 3. Element sample means ($\bar{X}$) and standard deviations (S.D.) by collection area at Dog Hill, Oregon. All values in parts per million.

Element		Collection Zone Z2N (n=5)	Z2S (n=5)	Z3 (n=5)
Th	$\bar{X}$	2.12	4.90	8.40
	S.D.	4.74	6.74	7.67
Pb	$\bar{X}$	40.38	42.58	41.98
	S.D.	2.90	3.15	3.44
Nd	$\bar{X}$	67.54	63.36	66.34
	S.D.	5.35	11.19	5.06
Pr	$\bar{X}$	23.08	15.36	17.90
	S.D.	11.10	2.87	8.18
Ce	$\bar{X}$	147.70	142.08	145.26
	S.D.	10.57	8.23	3.81
La	$\bar{X}$	67.02	70.92	65.60
	S.D.	3.64	5.16	4.27
Ba	$\bar{X}$	48.24	44.12	49.38
	S.D.	5.80	8.20	8.31
Nb	$\bar{X}$	31.96	36.02	36.24
	S.D.	3.31	6.18	3.89
Zr	$\bar{X}$	559.78	587.96	591.66
	S.D.	29.01	61.93	54.10
Y	$\bar{X}$	85.86	91.40	92.30
	S.D.	3.98	11.37	8.05
Sr	$\bar{X}$	3.10	3.46	2.02
	S.D.	2.28	1.64	2.22
Rb	$\bar{X}$	110.48	120.04	118.74
	S.D.	2.75	8.84	6.88
Ga	$\bar{X}$	22.14	22.54	21.20
	S.D.	3.48	2.26	4.75
Zn	$\bar{X}$	151.18	171.02	156.48
	S.D.	10.59	9.91	15.23
Cu	$\bar{X}$	3.12	11.46	2.22
	S.D.	2.10	16.78	2.18
Ni	$\bar{X}$	2.06	3.54	0.94
	S.D.	3.68	4.27	1.31

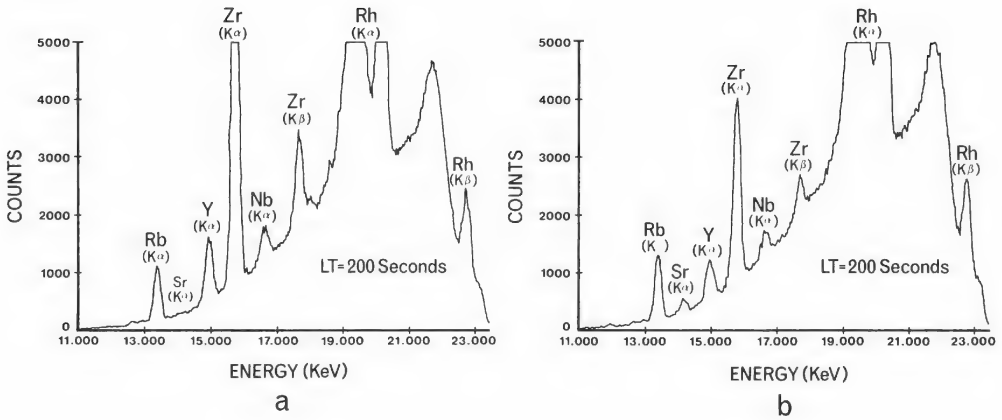

Figure 2. Energy dispersive x-ray fluorescence "fingerprint" of Dog Hill and Burns Butte volcanic glasses. a, "fingerprint" of an unmodified obsidian flake from Dog Hill (sample Z3-8); b, "fingerprint of an unmodified obsidian flake from Burns Butte (sample BB-6C).

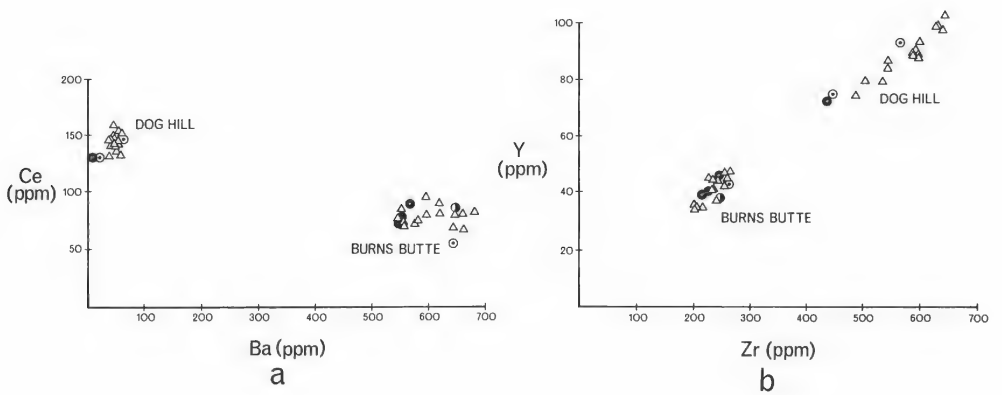

Figure 3. Scatter diagrams of Ce vs. Ba concentrations (Figure 3a) and Y vs. Zr concentrations (Figure 3b) for obsidian source specimens (open triangles) from Dog Hill and Burns Butte, Oregon. Circles represent values determined for prehistoric obsidian artifacts from archaeological sites 35CR29 (⊙), 35HA1300 (•) and P.P. & L. 42 (◑).

chance (at the 0.05α level), it can be concluded that these three areas at Dog Hill represent obsidian of the same geochemical type. As a result, measurements for all trace and rare earth elements were combined, yielding the summary statistics that appear in Table 2.

TABLE 4. Results of analysis of variance by element and collection area at Dog Hill, Oregon. Elemental data from Table 3. Critical value for $F_{2,12} = 3.88$ at 0.05 significance level.

Element	F-ratio	P_{chance}
Rb	3.027	0.085
Sr	0.658	0.540
Y	0.869	0.553
Zr	0.600	0.569
Nb	1.355	0.295
Ba	0.676	0.530
La	1.959	0.183
Ce	0.616	0.560
Zn	3.578	0.059

Comparison of these statistics (Table 2) shows that obsidian from Dog Hill can be distinguished from that occurring at Burns Butte on the basis of contrasts in Ce, Ba, Zr, Y, and Zn concentration. These inter-source differences are illustrated using bivariate scatter diagrams plotting Ce vs. Ba (Figure 3a) and Y vs. Zr (Figure 3b).

In order to test whether the results of the present analyses could profitably be applied to archaeological research, a small sample of obsidian artifacts from three archaeological sites in Harney and Crook Counties was analyzed and the results were compared to the trace element profiles generated for the Dog Hill and Burns Butte sources in east-central Oregon (Figure 3). As Figure 3 shows, these data fall within the range of trace element concentrations for source standards from both of these sources.[3] These results are of considerable interest because they document that these sources actually were exploited during prehistoric times, and that the glasses were conveyed over distances up to 100 kilometers from the parent geological sources. For example, three artifacts out of a total of 20 samples analyzed from the Beaverdam Creek site (35CR29) in the southern Ochoco Mountains (Figure 1, inset) matched the trace element configurations of Dog Hill and Burns Butte volcanic glass (Figure 3a, b). One specimen in this group, matched to the Dog Hill geochemical type, occurred in deposits 2,500-6,000 years old, while the other two artifacts were recovered in archaeological levels believed to date within the last 2,500 radiocarbon years (Erlandson and Moss 1984). Elsewhere, south of Burns Butte at the Horse Corral site (35HA1300, Figure 1) and at Sage Hen Hill, x-ray fluorescence analyses show that three artifacts were fashioned from Burns Butte obsidian, and one specimen was manufactured from obsidian of the Dog Hill geochemical type (Figure 3a, b). A single specimen analyzed from an archaeological site northwest of Burns Butte (P.P. & L. 42 on Figure 1; see Cole 1979:Appendix B, Map 26, Site 42) was fashioned from Burns Butte volcanic glass.

Although only a small number of east-central Oregon obsidian artifacts was analyzed, the results of this study clearly illustrate the potential for employing non-destructive quantitative analyses in establishing the likely parent geological source(s) for obsidian occurring in archaeological contexts. More generally, the agreement between the present analysis and previous destructive work (*cf.* Table 1) further supports the case that non-destructive analyses can yield concentration estimates in standard measurement units (*i.e.* parts per million or weight percent) suitable for interlaboratory comparisons (Hughes 1986a; see also Bieber *et al.* 1976, Harbottle 1982, Stross *et al.* 1983, Nelson 1984 for comments on the importance of using standard measurement units). The results of the present study indicate that it is now possible to use this non-destructive x-ray fluorescence technique to build a quantitative geochemical data base for Oregon volcanic glass sources and archaeological artifacts that can readily be used by researchers at other laboratories.

[3]After the Dog Hill and Burns Butte source analyses were completed, I learned of another natural obsidian occurrence located near Dog Hill at Willow Creek (35HA914, Figure 1). X-ray fluorescence analyses of ten specimens from this source showed that its trace element composition was statistically identical to Dog Hill. Consequently, prehistoric artifacts possessing trace element compositions diagnostic of the Dog Hill geochemical type could have been fashioned from obsidian obtained either from Dog Hill or Willow Creek.

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Seasonal Diets of Deer Mice on Bentonite Mine Spoils and Sagebrush Grasslands in Southeastern Montana

Abstract

Deer mice captured on bentonite mine spoils and sagebrush grasslands consumed mainly arthropods and seeds. Arthropod consumption was negatively correlated with availability and positively correlated with precipitation, indicating that deer mice apparently do not seek arthropods as a source of moisture. However, forb consumption was positively correlated with availability and negatively correlated with precipitation, indicating that deer mice eat forbs when available, but in increased amounts during periods of drought. Deer mice selected for specific types of arthropods and plants, but their selectivity may be partly an expression of the habitat.

Introduction

Deer mice (*Peromyscus maniculatus*) are common inhabitants of mine spoil environments (Verts 1957, Wetzel 1958, Sly 1976, Hansen and Warnock 1978, Hingtgen and Clark 1984), although little is known about their ecology in these habitats. Deer mice have been reported to be opportunistic, omnivorous animals, consuming a variety of foods depending on the habitat and season (Jameson 1952, Williams 1959, Flake 1973). Arthropods, seeds, and forbs are important in diets of deer mice, and these rodents have been reported to cause problems on seeded areas by consuming seeds of planted species (Everett *et al.* 1978). Seasonal differences in their diet have been largely attributed to changes in the availability of food resources (Johnson 1961, Whitaker 1966). However, few authors have presented data on food availability. This paper characterizes seasonal food habits of deer mice on bentonite mine spoils and unmined sagebrush grasslands, relates food selection to availability, and discusses potential impacts of deer mouse granivory and herbivory on revegetation efforts.

Study Area and Methods

This study was conducted in southeastern Montana, approximately 9 km west of the town of Alzada in southeastern Carter County. Elevations range from 1000 to 1100 m. The area receives an average of 37 cm of precipitation annually (National Oceanic and Atmospheric Administration 1976). Nearly 50 percent (18 cm) of the precipitation occurs between May and July. In 1979 and 1980, 26 and 35 cm of precipitation were received, respectively. Precipitation was lower than normal during most seasons of the study (Figure 1). The mean temperature is 7.8 C, ranging from an average of −6.4 C in January to 22.6 C in July (National Oceanic and Atmospheric Administration 1976).

Unmined sagebrush-grasslands are dominated by big sagebrush (*Artemisia tridentata*) with an understory of western wheatgrass (*Agropyron smithii*), and green needlegrass (*Stipa viridula*). Buffalograss (*Buchloe dactyloides*) and lichen (*Parmelia chlorochrae*) are other common species in the area. Rillscale (*Atriplex suckleyi*) is the most common plant on the bentonite mine spoils, regardless of the age or reclamation treatment. Western wheatgrass and crested wheatgrass (*Agropyron cristatum*) contribute slightly to the vegetal cover on the spoils; several other plants, including bromegrasses (*Bromus* spp.), foxtail barley (*Hordeum jubatum*), and lichen, are present as minor components of the plant cover on the mine spoils.

Twelve 60-x 60-m (0.36 ha) study sites were established: two on gently undulating unmined sagebrush grasslands, and 10 on bentonite mine spoils. The bentonite spoils ranged in age from

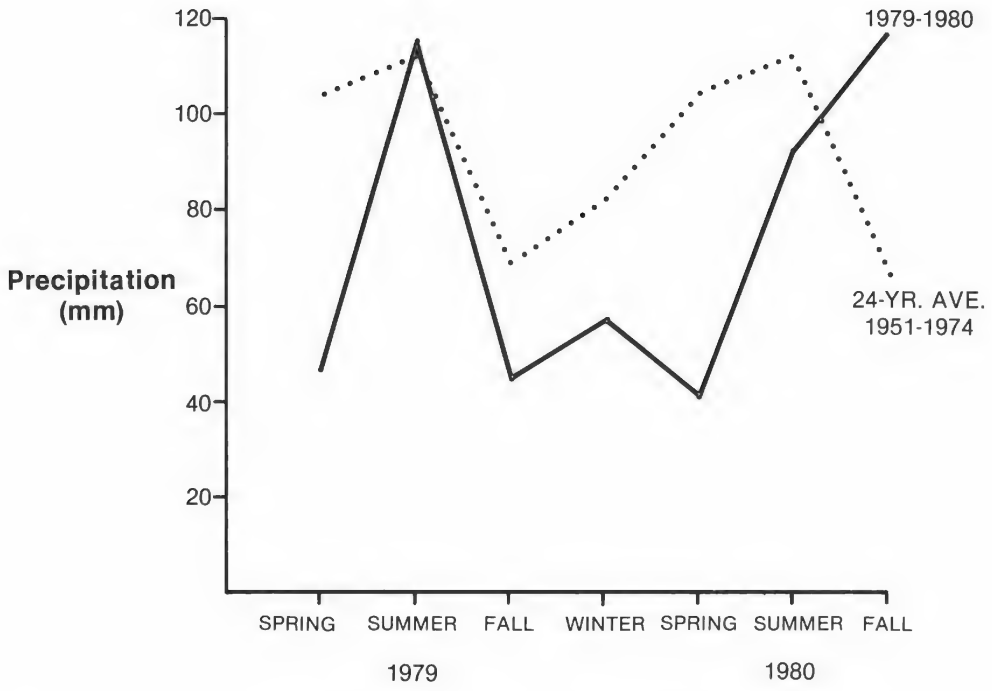

Figure 1. Total seasonal precipitation in 1979 and 1980 compared with average precipitation between 1951 and 1974, near Alzada, Montana.

1 to 28 years. Each bentonite pit and associated spoil pile cover less than 5 ha. Old bentonite spoils (12 to 28 years old) are steep and generally barren. More recent spoil piles have been recontoured, covered with a thin layer of topsoil, and seeded with a mixture of wheatgrasses (*Agropyron* spp.) and yellow sweetclover (*Melilotus officinalis*). However, excessive levels of salinity and sodium, severe soil compaction, and low precipitation often preclude the establishment of vegetation (Sieg *et al.* 1983).

Dietary Analysis

Fecal pellets were collected from deer mice captured in Sherman live traps. Thirty-six traps were arranged in a grid pattern with 10-m spacing on each site. After one night of pre-baiting, the traps were set for three consecutive nights every three weeks from May through October in 1979 and 1980. Rolled oats mixed with peanut butter was used as bait.

Fecal samples were collected from first-time captured animals, placed in paper envelopes and dried. The pellets were combined for each site and trap session, then divided into two equal samples. Invertebrates were identified by examining 40 fields per sample in a petri dish at 40 power magnification; then, one slide was made from each sample and 40 fields per slide were examined at 100 power magnification for identification and quantification of plant species (Sparks and Malecheck 1968). Frequency of occurrence data were converted to percent relative density (Fracker and Brischle 1944). Plant and arthropod samples were collected in the field and used as reference specimens.

Food Availability

The availability of foods was determined by sampling macroarthropod populations, plant

aboveground biomass, and plant canopy cover on each study site. Availability of arthropods was measured by the proportion of a particular arthropod group in the total capture. The relative abundance of ground-dwelling macroarthropods was estimated using 15-x 15-cm metal pitfall traps. Twelve cans were buried flush with the soil surface in a grid pattern with 15-m spacing on each site. The pitfall traps were opened every three weeks for three consecutive nights. The macroarthropods were collected, classified to order and family, and counted daily. Although this technique may underestimate less mobile arthropods and larvae (Thomas and Sleeper 1977), adequate results have been obtained for most species captured on this study area (Gist and Crossley 1973, Baars 1979).

Availability of forage was assumed to be equivalent to the proportion of a particular food plant in the aboveground biomass. Aboveground biomass was estimated each year at the peak of production (late July) by harvesting plants at ground level in 10 randomly located 20-x 50-cm quadrats on each of three permanent line transects on each site. Plant species were separated in the field, oven-dried in the laboratory at 60 C for 48 hours, and weighed.

Plant canopy cover was assumed to be a reflection of forb availability throughout the growing season. Plant canopy cover of forbs was estimated in 50 quadrats (20 x 50 cm) placed at 1-m intervals along permanent line transects (Daubenmire 1959). Three transects, each 50 m in length, were sampled on each site. Canopy cover was visually estimated as falling into one of seven cover classes: 0 = less than 1 percent cover, 1 = 1-5 percent, 2 = 5-25 percent, 3 = 25-50 percent, 4 = 50-75 percent, 5 = 75-95 percent, and 6 = 95-100 percent cover. Sampling was conducted three times a year, in late spring, midsummer, and late summer.

Statistical Analysis

One- and two-way (incorporating both years) analysis of variance and Tukey's multiple comparison procedure (Kleinbaum and Kupper 1978) were used to compare diets and food availability among sites and seasons. Spearman's rank order correlation coefficient and chi-square contingency tables (Steele and Torrie 1980) were used to compare dietary composition between years. Kendall's coefficient of concordance (Kendall 1970) was used to compare rank order of foods among site types.

Relative percentages of food items in the diets were compared to relative abundance in the field by chi-square analysis. Preference indices for arthropods were calculated by dividing the relative composition (based on relative density) of specific groups in the animal matter portion of the diet by the relative abundance of these arthropods in the field. Preference indices for plants were calculated by dividing the relative composition (based on relative density) of specific plants in the vegetal portion of the diet by the relative weight of these plants in the aboveground biomass (Krueger 1972).

Relationships between arthropods and forbs in the spring, summer, and fall diets in each year (dependent variables), and seasonal precipitation, forb cover, and arthropod availability (independent variables) were evaluated by all-possible regression analysis (Dixon 1983). The summer diet of the deer mice (dependent variable) was compared with total aboveground biomass (independent variable) for each year.

Results

Dietary Analysis

Arthropods and seeds were the major foods of deer mice captured during the study. Arthropods made up 52 percent and 75 percent of the diets in 1979 and 1980, respectively; seeds averaged 35 percent and 9 percent (Table 1). The most common arthropods in the diet were Hymenoptera (22 percent) and adult Coleoptera (15 percent and 18 percent). Rillscale seeds were commonly consumed in 1979, comprising 33 percent of the diet. American vetch (*Vicia americana*) was the most common forb eaten (2 percent and 7 percent). Grasses and shrubs made up a small portion of the diet in both years. Fungi (*Endogennae*) and algae were present in the feces in both years.

The rank order of food items was significantly correlated among site types ($W = 0.78$, $P < 0.005$), indicating that deer mice ate foods in the same relative proportions on the various sites. However, the rank order of food items in the diet was not significantly correlated for the two years ($r_s = 0.17$, $P > 0.10$), which indicated that the

TABLE 1. Major foods of deer mice (*Peromyscus maniculatus*) on bentonite mine spoils and sagebrush-grass rangelands near Alzada, Montana (N = 192).

Food Item	% Relative Density 1979 ($\bar{x}$ ± SE)[1]	1980 ($\bar{x}$ ± SE)[1]
Arthropods		
Araneida	0.2 ± 0.1	2.7 ± 1.6
Coleoptera adult	17.5 ± 2.3	15.4 ± 2.7
Coleoptera larvae	1.3 ± 0.5	2.4 ± 0.8
Diptera	0	9.8 ± 1.8
Hymenoptera	22.2 ± 2.3	22.4 ± 3.7
Lepidoptera	0.4 ± 0.1	7.5 ± 2.1
Orthoptera	0.1 ± 0.05	8.2 ± 2.0
Unknown adult	2.3 ± 0.7	2.6 ± 1.5
Unknown larvae	8.1 ± 1.0	3.6 ± 1.1
Total	(52.1 ± 3.1)	(75.0 ± 2.8)
Seeds		
Atriplex suckleyi	32.9 ± 2.5	2.6 ± 0.3
Chenopodium spp.	0.01 ± 0.01	1.0 ± 0.2
Plantago sp.	0	2.2 ± 0.6
Unknown seeds	1.2 ± 0.4	3.2 ± 0.2
Other seeds	0.4 ± 0.1	0.1 ± 0.1
Total	(34.5 ± 2.8)	(9.1 ± 0.5)
Grasses		
Bromus spp.	0.8 ± 0.1	0.3 ± 0.1
Other grasses	1.3 ± 0.4	0.4 ± 0.1
Total	(2.1 ± 0.3)	(0.7 ± 0.1)
Forbs		
Atriplex suckleyi	1.3 ± 0.3	0.8 ± 0.2
Vicia americana	2.0 ± 0.3	6.8 ± 1.8
Other forbs	0.8 ± 0.2	3.4 ± 0.5
Total	(4.1 ± 0.3)	(11.0 ± 0.6)
Shrubs		
Artemisia tridentata	1.9 ± 0.02	1.9 ± 0.1
Other shrubs	0.7 ± 0.1	0.1 ± 0.1
Total	(2.6 ± 0.3)	(2.0 ± 0.2)
Algae	1.4 ± 0.8	0.9 ± 0.4
Fungi (*Endogennae*)	2.9 ± 0.9	1.6 ± 0.7

[1]Mean ± standard error.

deer mice did not eat foods in the same relative proportions during the two years. The dietary shift ($P < 0.001$) between years included a decrease in seed consumption and an increase in invertebrates eaten in 1980 (Table 1). Rillscale seeds decreased from 33 percent of the diet in 1979 to 3 percent in 1980. Diptera arthropods were present in the deer mouse diet (10 percent) only in 1980.

Seasonal trends in arthropod consumption were similar in both years, with peak consumption occurring in the summer (June and July) (Figure 2). Fewest arthropods were consumed in spring. However, seasonal trends for seed consumption differed ($P < 0.05$) between years. Seed consumption was highest in the spring of 1979, and lowest in summer (Figure 3). Seed consumption increased during the 1980 study period, with the peak consumption occurring in the fall. Grasses and shrubs were consumed in small amounts in all seasons.

Food Availability

Macroarthropods. A total of 1187 macroarthropods were captured in 1979, while numbers decreased ($P < 0.01$) to 530 in 1980. Peak captures occurred in the spring of 1979 (April and May), and in the summer of 1980 (June and July) (Figure 2). The rank order of common macroarthropods was significantly correlated among sites ($W = 0.81$, $P < 0.005$), indicating that various arthropods were available in the same relative amounts on the twelve sites.

Ground beetles and other Coleoptera, crickets (Orthoptera), and ants and wasps (Hymenoptera) were the most commonly captured macroarthropods on the study area, followed by wolf spiders (Araneida) and mites (Acarina). Daddylonglegs (Opiliones), millipedes (Diplopoda), and true bugs (Hemiptera) each contributed less than 5 percent to the total capture. Scorpions (Scorpionida) and butterflies and moths (Lepidoptera) were captured in low numbers. The relative abundance of the arthropod types captured on the study area differed significantly ($P < 0.001$) from the percentage of these arthropods in the diet of the deer mice. Dipterans and Lepidopterans were preferred arthropods only in 1980; Hymenopterans were slightly preferred foods in both years (Table 2).

Plants. In 1979, aboveground biomass averaged 215 kg/ha; in 1980 the average production decreased ($P < 0.05$) to 121 kg/ha on the twelve study sites. Important plant species on the study area, in terms of percent relative weight, were rillscale, wheatgrasses, lichen, buffalograss, and green needlegrass (Table 3). The relative composition of prominent plant species differed significantly ($P < 0.05$) from the relative density of these plants in the diets of deer mice captured on the study area. Rillscale and lichen had the highest preference indices in 1979; American

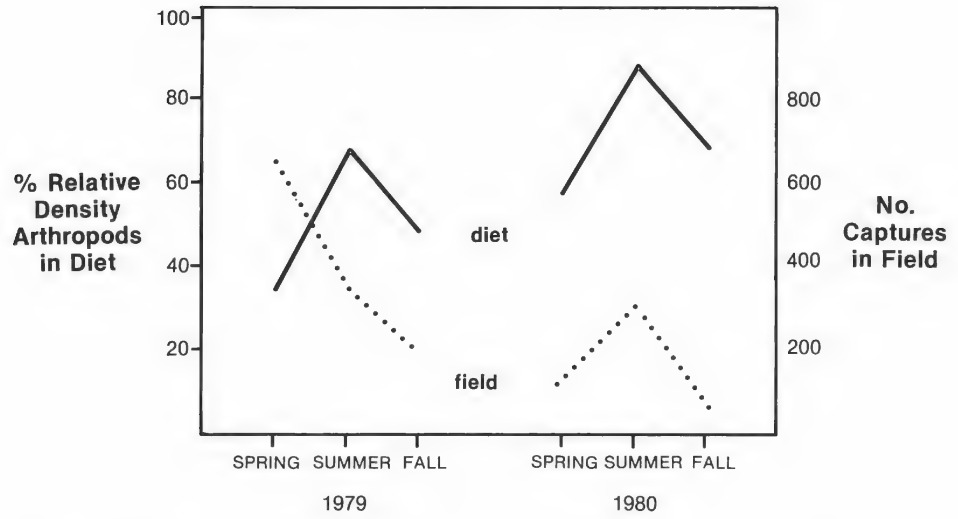

Figure 2. Relative amounts of arthropods in deer mouse diets compared with seasonal arthropod captures on bentonite mine spoils and sagebrush grasslands near Alzada, Montana in 1979 and 1980.

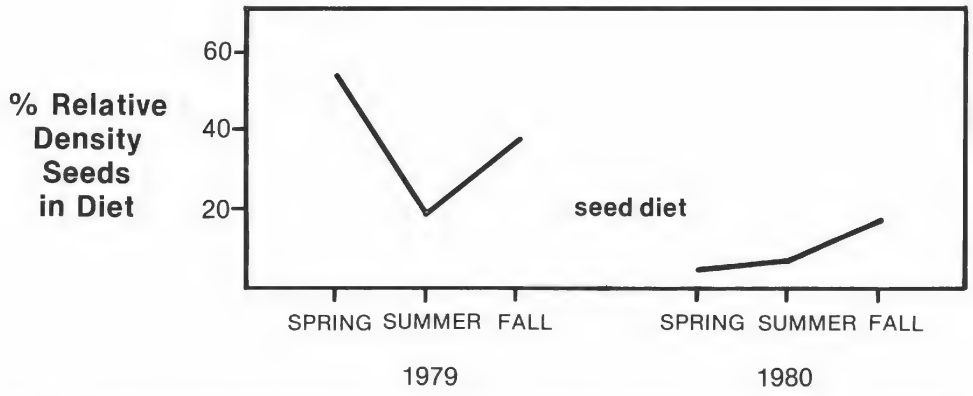

Figure 3. Relative amounts of seeds in deer mouse diets on bentonite mine spoils and sagebrush grasslands near Alzada, Montana in 1979 and 1890.

vetch and rillscale were the most preferred species in 1980. Wheatgrasses and buffalograss were among the least preferred plants in both years (Table 3).

Plant canopy cover of forbs averaged less than 10 percent during all seasons of the two-year study. Forb cover peaked in the fall of 1979, and in the summer of 1980 (Figure 4).

Discussion

Arthropods, seeds, and forbs are common components of deer mouse diets, although their relative proportions vary regionally. The high proportion of arthropods in this study is consistent with several studies (*i.e.*, Dusek and McCann 1975, Halford 1981, Hingtgen and Clark 1984), although species composition varies from some

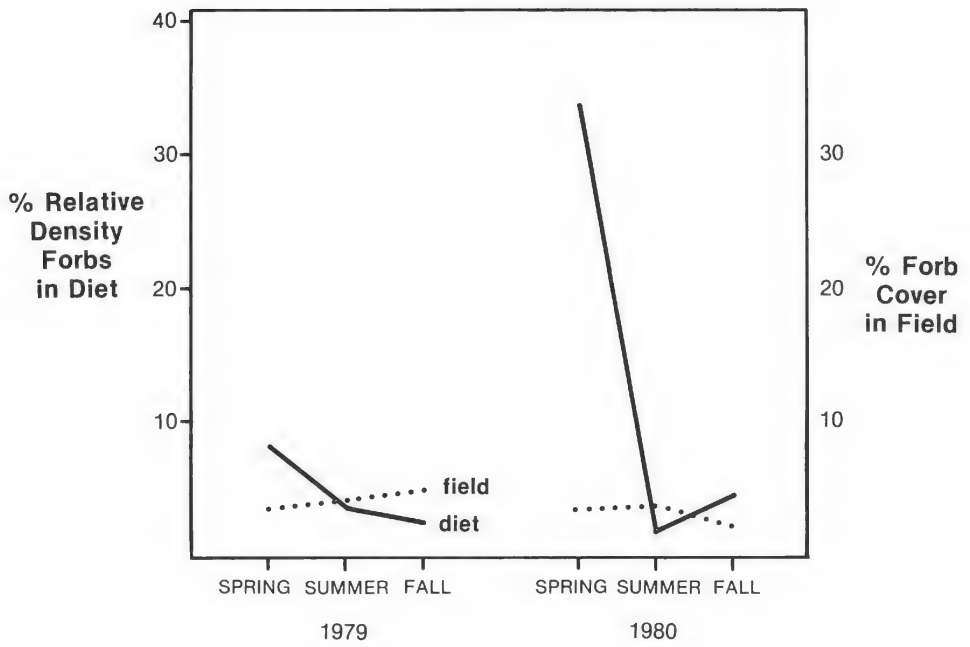

Figure 4. Relative amounts of forbs in deer mouse diets compared with average seasonal forb cover on bentonite mine spoils and sagebrush grasslands near Alzada, Montana in 1979 and 1980.

TABLE 2. Percent relative composition and deer mouse preference indices for arthropods captured on bentonite mine spoils and sagebrush-grasslands near Alzada, Montana, in 1979 and 1980.

	1979		1980	
Group	% of Capture	Preference Index	% of Capture	Preference Index
Coleoptera	29.1	0.6	30.2	0.6
Orthoptera	19.9	0.1	38.7	0.2
Hymenoptera	20.4	1.1	12.6	1.8
Araneida	14.7	0.1	9.4	0.3
Acarina	6.0	0	2.3	0
Opiliones	3.4	0	2.6	0
Diplopoda	4.0	0	0.8	0
Lepidoptera	0.8	0.4	1.3	5.7
Hemiptera	1.3	0	0.9	0.4
Diptera	0	0	0.1	9.8
Unknown	0	-	1.1	-

TABLE 3. Percent relative weight in aboveground biomass and deer mouse preference indices for plants on bentonite mine spoils and sagebrush-grasslands near Alzada, Montana, in 1979 and 1980.

Plant	1979		1980	
	% by Weight	Preference Index	% by Weight	Preference Index
Atriplex suckleyi	25.8	22.1	42.1	10.4
Agropyron spp.	28.3	0.1	22.8	0.1
Parmelia chlorochrae	7.4	5.7	9.3	3.2
Stipa viridula	8.2	0	2.5	0
Buchloe dactyloides	3.4	0	7.2	0
Bromus spp.	3.2	4.8	1.5	7.4
Vicia americana	0.8	3.9	0.4	22.3

studies. Lepidopterans (Flake 1973) and Orthopterans (Dusek and McCann 1975) were more important food sources in other studies than Coleopterans and Hymenopterans. Deer mice are known for their granivorous food habits, and have been blamed for consuming planted seeds (*i.e.,* Everett *et al.* 1978). However, a preference for *Atriplex* seeds has not previously been reported. Big saltbush (*A. lentiformis*) and fourwing saltbush (*A. canescens*) were among least preferred plants offered to deer mice by Everett *et al.* (1978). Forbs are generally minor components in deer mouse diets, but may comprise the majority of the diet in some habitats (Goodwin and Hungerford 1979). American vetch has not previously been reported as a preferred food item, although sainfoin (*Onobrychis viciaefolia*), also a legume, was a preferred food of deer mice on seeded coal spoils in Wyoming (Hingtgen and Clark 1984).

Yearly and seasonal variations in the deer mouse diet are commonly reported, and are generally attributed to changes in availability of the food resources (Whitaker 1966). However, in this study, arthropod consumption was higher in 1980 than in 1979, in spite of substantial declines in macroarthropod captures in 1980. Further, arthropod consumption was negatively correlated ($r = -0.28$, $p = 0.014$) with arthropod availability, indicating that the mice did not necessarily consume arthropods in relation to their availability. Arthropod consumption was positively correlated with precipitation ($r = 0.49$, $p = 0.0001$), supporting recent conclusions of Meserve (1976) and Haufler and Nagy (1983), that deer mice apparently do not seek arthropods as a source of moisture. Possibly, because of the higher caloric content of arthropods (5.8 kcal/g), compared to seeds (4.4 kcal/g) and green vegetation (4.1 kcal/g) (French *et al.* 1976), deer mice sought out arthropods to meet minimal nutritional requirements, particularly when plant materials were less available.

The increase in forb consumption from 1979 to 1980 may be attributed to dry conditions, especially during the spring of 1980. Forb consumption was positively correlated ($r = 0.43$, $p = 0.001$) with total forb canopy cover, but negatively correlated with precipitation ($r = -0.40$, $P = 0.001$), indicating that deer mice consumed forbs when available, but in increased amounts during periods of drought. Other authors have suggested the importance of green vegetation as a source of moisture (Jones *et al.* 1983), and the potential role of green vegetation in the diet on the reproductive capacity of some small mammals (Reichmann and Van De Graff 1975).

Seed consumption declined from 1979 to 1980, and at least for rillscale seeds, was likely related to availability. During drought periods, rillscale was short in stature and produced fewer seeds. Flake (1973) reported that deer mice depended on seeds in times of insect scarcity, but in this study, the greatest use of seeds was in the spring of 1979, when insects were highly available.

Deer mice have been reported to be very opportunistic feeders, readily consuming new foods (Johnson 1961), and reflecting the availability of various foods in their diets. However, if deer mice in this study were totally opportunistic, they should have selected foods in proportion to the availability of the food items. To the contrary, the deer mice appeared to show some dietary selectivity, as indicated by high preference indices for some uncommon plants (*i.e.,* bromegrasses and American vetch) and lower indices

for some common plants (*i.e.*, wheatgrasses). Deer mice on our study area also appeared to exhibit some selectivity in regards to arthropods. Crickets (Orthopterans) were highly available, yet were apparently not preferred food items, based on low preference indices. Availability of Lepidopterans and Dipterans is more difficult to measure with the use of pit traps, but assuming their capture rates are a relative approximation of availability, deer mice in our study showed some preference for these arthropods, at least in 1980. Limited food resources in 1980 provided a good test of the "opportunistic hypothesis," and high preference indices in that year suggest that deer mice actively searched out some foods, and therefore may not be totally opportunistic in their feeding behavior.

It is unlikely that deer mice pose a serious threat to revegetation success on bentonite mine spoils. Deer mice in this area relied heavily on arthropods, and to a lesser extent on plant materials. Wheatgrasses are a major component of seed mixtures used in this area, and deer mice showed low preference for these grasses, although wheatgrasses were important in the total plant biomass on the study area. The most significant negative impact on revegetation efforts may be on some native legumes, such as American vetch, which was highly preferred by deer mice in our study. Hingtgen and Clark (1984) concluded that deer mice on Wyoming coal spoils negatively affected the establishment of sainfoin.

Conversely, deer mice may be beneficial to the establishment of some plants on bentonite mine spoils, and may help control some undesirable plants. Rothwell and Holt (1978) proposed that deer mice on recent mine spoils are important as vectors of vesicular-arbuscular mycorrhizal fungi. The presence of mycorrhizae in the feces of deer mice captured on bentonite mine spoils was an indication of the role these animals play in the dispersal of endophytes essential to the growth and development of many plants. Further, the high preference for bromegrasses is an indication that deer mice may help curb the invasion of undesirable bromegrasses on the mine spoils.

Perhaps deer mice should be called "selective opportunists." On this study area, deer mice readily exploited new food resources on the bentonite mine spoils, but did not always consume foods in the same relative proportion to availability. Nutritional needs, including water requirements, may influence the dietary habits of these small mammals, possibly causing them to seek out forbs during periods of drought. Future research comparing the dietary habits of deer mice with the availability of various food resources may show that deer mice are more selective in their feeding behavior than previously reported, but the expression of selectivity may be determined in part by the habitat.

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Biomass Regression Equations for Understory Plants in Coastal Alaska: Effects of Species and Sampling Design on Estimates

Abstract

Biomass prediction equations were developed for 9 species of shrubs and trees and 16 species of herbs and bryophytes from 24 coastal sampling sites in southeastern Alaska. Samples were taken from clearcuts and from second-growth and old-growth forests. Stem diameter was the best predictor of shrub biomass. For all herbs, except some ferns and members of the Liliaceae, percentage of ground cover was the best predictor. Regression equations accounted for 74 to 99 percent of biomass variation, and differences between slopes of most equations for different species were highly significant. Slopes and y-intercepts were generally related to vegetation sere or autecology of the species. Species with monolayer canopies generally accumulated less biomass per stem or ground area than species with multilayered canopies. Date of sample collection (1 July to 1 Sept.) was not related to biomass. From 10 to 15 4-m^2 plots or 30 to 60 1-m^2 plots, systematically placed, were needed for precise estimates of understory biomass in mature or old-growth forests. In recently disturbed vegetation, more than 15 4-m^2 or 60 1-m^2 plots were needed for precise estimates. Plots 4-m square were more efficient than plots 1-m or 0.1-m square for estimating biomass to a given level of precision.

Introduction

Despite widespread use of regression equations for biomass estimates, the variation among species in plant dimension-biomass relationships has been little examined. If patterns in this relationship can be related to the general morphology or autecology of different species, equations selected for biomass estimates will be more appropriate, more field efficient, and less biased.

Most emphasis has been placed on large, dominant, woody species in which much of the forest biomass is accumulated, yet such species may not characterize ecosystem dynamics as well as understory vegetation (< 2 m tall), which responds to subtle changes in stand structure, microclimate, and edaphic factors (e.g., Anderson *et al.* 1969). Information on understory productivity may be critical for understanding processes such as nutrient cycling and animal foraging. Also, large-scale destructive sampling of vegetation biomass is more practical for the understory than overstory. These factors make desirable an investigation of the relationship of plant genetics and environment to plant dimensions and biomass.

Parameter coefficients for individual species and, in some cases, for particular growing sites may vary widely, as relationships between plant biomass and size class are empirically derived (Agee 1983). For unbiased biomass estimates, relationships of biomass and plant dimensions should be developed for each species common to a given habitat type or productivity class. Biomass regression equations are often used interchangeably among species with little theoretical basis, and some understory strata are wholly ignored.

This study examines biomass and—where practical—productivity of shrubs, herbs, ferns, mosses, liverworts, and lichens that are widespread in the Pacific Northwest, Canada, and southern Alaska. Objectives were: 1) to determine easily measured variables that best relate to biomass and productivity of understory vegetation in coastal Alaska, 2) to develop equations for the relationships of plant size-class to biomass of each species, and 3) to characterize the variability of biomass equations in differing environments and with differing methodologies.

Methods

Site Selection

The 24 sites for destructive sampling were selected for a range of environments within the *Picea sitchensis-Tsuga heterophylla* (Sitka spruce-western hemlock) forests of southeast Alaska (Table 1); for homogeneity of vegetation, slope, and aspect, and for ease of access. Each was below 150 m elevation on well-drained gentle

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slopes (< 20 percent) and included closed-canopy (> 70 percent mean canopy cover) or clearcut forests. Most sites had been previously sampled for studies of secondary succession and overstory-understory relationships (Alaback 1982a, 1982b).

Biomass samples were taken over a 2-month period rather than for the estimated period of "peak understory biomass" because of the short Alaskan summer and the distance between sites, more than 400 kilometers (Grigal *et al.* 1976). One site was sampled on 29 June, 29 July, and 28 August in order to test whether the time scheme biased estimates of plant biomass. Development of a relative index of the date of sample collection within the growing season of a site further identified the effect of phenology on biomass estimation. The relationship of growing season to latitude was developed from available meteorological data (National Oceanographic and Atmospheric Administration 1978). Time and length of the growing season was then estimated for each study site.

Species Selection

Relative abundance of each understory vegetation species was estimated on 60 sites over a broad range of stand age-classes, geographic locations, and edaphic conditions (Alaback 1982b). Seventy-eight species were found. More than 70 percent of the ground cover was occupied by the 10 most abundant species. Aboveground biomass of all vascular plant species averaging more than 0.1-percent ground cover (relative to other vegetation rather than to total land area) was sampled—seven woody shrub species, nineteen herbaceous or low-growing shrub species, and the nine most abundant bryophyte and lichen species.

Sampling Procedure

From low-growing shrubs such as *Cornus canadensis* (bunchberry) and *Rubus pedatus* (trailing bramble), only vertical shoots (not rhizomes or runners) were sampled. Woody-shrub shoots were cut flush with the forest litter layer. Woody shrub shoot height, basal diameter, and vigor class were tested for their relationship to biomass. Vigor was defined as the percentage of live twigs and branches per individual shrub canopy. Primary productivity of deciduous herbs was assumed to be equal to aboveground biomass, and that of shrubs was measured as the biomass of current annual twigs and deciduous foliage. Foliar production of evergreen species, which normally retain leaves for three years, was assmued to be one-third that of the foliar biomass. Moss samples, clipped at ground level, did not include decomposing, nonyellow or nongreen parts.

Specimens were collected between 1 July and 1 September, 1977 to 1984. During the first year, emerging stems of all plants rooted within 1-m^2 quadrats randomly located throughout several study sites were measured and collected for drying, a scheme that resulted in oversampling of the most abundant species. Subsequently, species and size-classes on each site were determined first, then each was randomly sampled for a more equitable distribution.

First, selected specimens were measured nondestructively, then samples were collected and components separated into paper bags for drying and weighing. Some samples were taken intact into the laboratory for more efficient separation. All were dried at least 24 hours at 70°C, then stored in plastic bags to retard absorption of ambient humidity. Weight was recorded to the nearest 0.001 g on specimens of less than 10 g and to the nearest 0.1 g on those greater than 10 g.

All plants in each 1-m^2 or 4-m^2 plot in each of the 60 previously studied sites (Alaback 1982a, 1982b) were measured preparatory to determining the effects of sampling intensity on understory biomass estimates. A random-number generator selected successively increasing numbers of plots for the estimates in each stand. Four runs with four sets of randomly chosen plots were made for each stand in order to characterize variability with increasing sampling intensity. Sampling-area curves, a simple extension of the concept of a species area curve (Cain 1938), were then plotted for each of the 60 sites. Sample variance and number of plots necessary for estimates within 10 percent of the mean were calculated for all sites (Cochran 1963).

Parameter Selection

Biomass-equation parameters were selected for precision of prediction and maximum field efficiency. If plant densities varied widely, more than one set of independent variables was used for each species. Parameters for biomass estimation were initially chosen for dense stands of

western hemlock (*Tsuga heterophylla*) that often have a sparse understory, especially in seral stands (Alaback 1982a). When more dense vegetation was sampled, more expeditious but often less precise estimation techniques were developed. *Gymnocarpium dryopteris* (oak fern) and *Streptopus roseus* (twisted stalk) are two species that required more than one sampling strategy. In depauperate stands, all fronds or shoot lengths in a 1-m^2 plot were measured; in open, mesic forests, where these species often formed dense thickets, the relation of the percentage of ground cover to biomass was used in the regression model. The few biomass studies that have included bryophytes have employed core sampling or area-based destructive sampling rather than dimension analysis (Forman 1969, Clymo 1970). Dimension analysis was used here for maximum field efficiency and for compatibility with data collection for other species.

Statistical Analysis

Regression equations were developed by means of the SPSS statistical subroutines on the CDC CYBER computer at Oregon State University and the MICROSTAT software on an 8-bit microcomputer. For most species, two models gave the best results: the log-log transformation or the simple (untransformed) linear model (Draper and Smith 1966). Since equations applied to depauperate vegetation often predict negative biomass at the low extreme of independent variables (i.e., percentage of ground cover < 5 percent), separate equations were developed for the low range when they improved accuracy. Final equations were adjusted for logarithmic bias (Baskerville 1972).

Comparisons of regression equations were made by calculating F statistics from a full-parameter regression model and a series of reduced models. In the full model, the slopes and y-intercepts of all regression equations were included; in reduced models, only those for regression equations of a species subset were included. If significant differences were detected, pairwise comparisons were made of individual equations by changing the design matrix to include only those equations (Neter and Wasserman 1974).

Results

Percentage of ground cover was linearly related to the biomass of most species. Only species with substantial height variation showed a curvilinear relationship (Tables 2, 3). Virtually all regressions based on stem diameter or shoot length were curvilinear, a pattern in general agreement with other dimension analyses of shrubs and trees (Brown 1976, Gholz *et al.* 1979, Stanek and State 1978, Smith and Brand 1983). At the low extreme of ground-cover area (0-10 percent), biomass also had a curvilinear relationship. This change in equation form with low cover may relate to changes in plant morphology with age and size, factors less important when the plants are mature and occupy more area.

Effects of Species

Woody species. Because of the vertical dimension and variable structure of woody shrub species, measures of abundance such as percentage of ground cover or frequency of occurrence are usually imprecisely related to biomass (Table 4). Overall, the amount of shrub cover bore a good relationship to biomass; however, the same amount corresponded to drastically different biomass density in clearcuts and old-growth (Figure 1). A cover-based biomass regression equation is not a good general-purpose equation for a range of site conditions, as it will give highly imprecise estimates. Twenty-three to eighty percent of the variation in shrub biomass was accounted for by the percentage of cover measured on 22 sites in 1978. The mean square error (MSE) of biomass estimates was 1.5 to 15 times greater with regression equations based on percentage of cover than with those based on stem diameter (Tables 2, 3). Plot size also made a substantial difference. Large, clumped species such as *Menziesia ferruginea* (rusty menziesia) had a significant relationship to biomass on 4-m^2 plots but an insignificant one on smaller plots ($P = 0.05$).

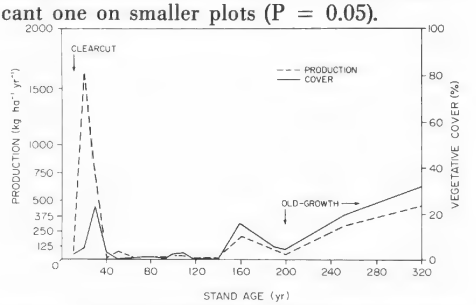

Figure 1. Relation of productivity of *Vaccinium alaskaense* to percentage of ground cover over a chronosequence of stands (Alaback in press).

TABLE 1. Characteristics of 24 sites selected for destructive biomass sampling in southeast Alaska.[1]

Location	Age Class[2]	Site Index ($m \cdot 100\ yr^{-1}$)	Elevation (m)	Stand Origin
Clark Bay	Clearcut	--	38	Logging
Douglas Bay	Clearcut	36	5	Logging
Harris River[3]	Clearcut	38	67	Logging
Maybeso Valley	Clearcut	40	91	Logging
Thomas Bay	Clearcut	31	8	Logging
Tuxekan Island	Clearcut	30	30	Logging
Agate Beach	Mature	31	7	Logging
Bartlett Hospital	Mature	37	30	Windthrow
Edna Bay	Mature	40	30	Logging
Kanulku Bay	Mature	32	30	Fire
Kindergarten Bay	Mature	30	15	Fire
Mitchell Bay	Mature	37	25	Fire
Old Franks	Mature	37	61	Fire
Old Franks	Mature	40	30	Fire
Saks Cove	Mature	36	30	Logging
Point Barrie	Mature	38	33	Logging
Point White	Mature	33	30	Logging
South Zarembo Is.	Mature	37	23	Logging
Virgin Bay	Mature	40	122	Logging
West Zarembo Is.	Mature	42	7	Logging
Clark Bay	Old-growth	35	45	Unknown
Hawk Inlet	Old-growth	--	Varies	Unknown
Lemon Creek	Old-growth	--	46	Unknown

[1]See Alaback (1982b) for a more complete description of these sites.

[2]Clearcut = forests less than 40 years old and of logging origin; mature = forests 40-250 years old; old-growth = stands with codominant trees > 250 years old (Alaback 1982a).

[3]Samples were taken from both control and precommercially thinned sections of the stand.

TABLE 2. Relation of percentage of ground cover to total aboveground biomass of three representative shrub species. Cover estimates are based on averages of 10 to 15 4-m^2 plots or 30 to 60 1-m^2 plots. A linear regression model was used.

Shrub Species	B_0	B_1	n	r^2	MSE	Range of Cover (%)
		4-m^2 plots				
Vaccinium alaskaense	2.4659	0.4123	22	0.228	30.563	0-26
Menziesia ferruginea	0.0905	1.5497	22	0.791	2.840	0- 5
Rubus spectabilis	0.5631	0.8025	22	0.555	6.875	0-16
		1-m^2 plots				
Vaccinium alaskaense	−7.220	17.307	15	0.559	147.33	0-42
Menziesia ferruginea	9.5272	−1.1535	15	0.000	20.865	0- 5
Rubus spectabilis	14.4183	12.5609	15	0.705	50.703	0-66

TABLE 3. Equations for predicting biomass[a] of woody shrubs and understory trees, low-growing shrubs, herbaceous vascular plants, ferns, bryophytes, and foliose lichens.

Species	Y_i[b]	$\hat{B}_o$	$\hat{B}_1$	X_i[c]	Units	n	r^2	MSE	Range X
				Woody shrubs and understory trees					
Menziesia ferruginea	prod	−3.9782	2.4244	ln dia	mm	24	0.83	0.652	1-24
	wood	−4.1260	3.1899	ln dia	mm	24	0.93	0.472	1-24
	fol	−3.2229	1.9287	ln dia	mm	15	0.79	0.440	1-24
	twig	−7.5778	3.0260	ln dia	mm	10	0.74	1.845	1-24
Oplopanax horridum	wood	−6.7588	3.6530	ln dia	mm	21	0.84	0.710	5-30
	fol	−5.1580	2.8904	ln dia	mm	16	0.89	0.260	5-30
	twig	−4.9413	2.3650	ln dia	mm	18	0.84	0.318	5-30
Ribes laxiflorum	twig	−0.0842	0.0556	dia	mm	6	0.87	0.002	2- 7
	wood	−1.8576	3.3567	dia	mm	6	0.80	0.158	2- 7
	fol	−3.2735	1.2329	dia	mm	6	0.81	0.158	2- 7
Rubus spectabilis	prod	−3.7189	2.8406	ln dia	mm	60	0.72	0.578	1-25
	wood	−2.5536	2.5467	ln dia	mm	35	0.76	0.308	2-25
	fol	−2.0270	1.8840	ln dia	mm	21	0.77	0.382	2-25
	twig	−2.7389	2.0899	ln dia	mm	21	0.86	0.260	2-25
Sambucus canadensis	prod	−4.5228	2.8875	ln dia	mm	18	0.92	0.306	2-29
	wood	−6.0146	3.8064	ln dia	mm	21	0.92	0.570	2-29
	fol	−4.8793	2.9225	ln dia	mm	18	0.92	0.343	2-29
	twig	−6.2614	2.0991	ln dia	mm	20	0.85		
							4	0.348	2-29
Tsuga heterophylla	biom	−2.3777	2.8080	ln dia	mm	205	0.99	0.123	1-29
	fol	−2.9876	2.2490	ln dia	mm	110	0.97	0.244	1-29
	wood	−3.0539	2.7891	ln dia	mm	110	0.98	0.281	1-29
Vaccinium alaskaense -ovalifolium	prod	−3.3489	1.9657	ln dia	mm	191	0.75	0.673	1-26
	wood	−2.8911	2.7765	ln dia	mm	68	0.92	0.472	1-26
	fol	−2.5927	1.7790	ln dia	mm	16	0.79	0.870	1-26
	twig	−3.0235	1.5324	ln dia	mm	19	0.74	0.885	1-26
V. parvifolium	prod	−3.2121	2.1207	ln dia	mm	27	0.83	0.557	1-21
	wood	−2.5582	3.0842	ln dia	mm	19	0.97	0.334	1-21
	fol	−2.7705	2.0208	ln dia	mm	20	0.75	1.644	1-21
	twig	−3.1062	1.7640	ln dia	mm	14	0.85	0.763	1-21
	biom[d]	−0.7809	0.9532	ln cov	%	12	0.82	0.245	1-10
				Low-growing shrubs and herbaceous vascular plants[e]					
Clintonia uniflora	biom	−9.4249	2.4713	ln len	cm	59	0.96	0.042	6-18
Coptis aspleniifolia	biom	0.7780	0.3420	cover	%	19	0.87	0.021	2-40
	biom	−1.1096	1.1501	ln cov	%	12	0.71		
							7	0.135	1-10
Cornus canadensis	biom	−0.6950	0.5360	cover	%	20	0.95	0.032	3-60
	biom	0.2180	0.0440	cover^2	%	12	0.52	0.024	1-10
Lysichiton americanum	biom[d]	−12.40							
		25	3.2564	ln len	cm	38	0.84		
							1	0.767	5-145
Maianthemum dilatatum	biom	−1.3370	0.4080	cover	%	15	0.93	0.083	1-97
	biom	0.009	0.324	cover	%	9	0.99	0.001	1-15
Moneses uniflora	biom	1.667	0.3950	cover	%	8	0.89	0.150	1-25
Rubus pedatus	biom	2.1030	0.1640	cover	%	19	0.84	0.020	1-60
	biom	1.202	0.0300	cover^2	%	10	0.77	0.007	0-11
Streptopus amplexifolius	biom	−9.6545	2.3971	ln len	cm	26	0.99	0.074	4-91
S. roseus or	biom	−8.1465	1.9410	ln len	cm	28	0.89	0.000	7-24
S. streptopoides	biom	−0.135	0.0950	cover	%	21	0.96	0.191	3-90
	biom	0.021	0.0100	cover^2	%	7	0.70	0.074	3-10
Tiarella trifoliata	biom	−3.0090	0.8030	cover	%	22	0.95	0.145	1-75
	biom	0.7857	0.0379	cover^2	%	13	0.66	0.013	0-10

Table 3 continued

Species	Y_i[b]	$\hat{B}_0$	$\hat{B}_1$	X_i[c]	Units	n	r^2	MSE	Range X
				Ferns[e]					
Asplenium viride	biom	−9.3292	2.2520	ln len	cm	30	0.98	0.000	13- 42
Athyrium filix-femina	biom	−9.9656	2.3740	ln len	cm	32	0.98	0.000	18-147
Blechnum spicant	biom	−7.4742	1.8480	ln len	cm	78	0.78	0.053	14- 56
Dryopteris austriaca	biom	−8.8097	2.2050	ln len	cm	229	0.98	0.000	4- 95
Gymnocarpium dryopteris	biom	−9.2541	2.2105	ln len	cm	55	0.97	0.053	5- 50
	biom[d]	−3.5235	1.4830	ln cov	%	20	0.97	0.073	5-100
Polystichum munitum	biom	−8.6306	2.2591	ln len	cm	32	0.95	0.090	8-106
Thelypteris phegopteris	biom	−8.9893	2.2815	ln len	cm	13	0.97	0.000	13- 27
				Bryophytes and foliose lichens					
Stokesiella oregonum	biom	12.8190	1.2330	cover	%	8	0.86	0.028	2-90
Hylocomium splendens	biom	0.4446	1.0968	ln cov	%	30	0.91	0.053	1-90
Jungermannia lanceolata	biom	−6.6614	1.8181	ln cov	%	28	0.89	0.159	1-88
	biom	0.0000	0.7120	cover	%				1-22
Lobaria oregona	biom	−2.7774	1.7255	ln rad	cm	40	0.90	0.207	1-16
Plagiothecium undulatum	biom	−0.6580	0.8800	cover	%	17	0.81	0.950	1-15
Pogonatum macounii	biom	−3.6120	1.7750	cover	%	12	0.94	0.987	1-90
	biom	0.000	0.5710	cover	%				1- 3
Rhizomnium glabrescens	biom	7.0710	0.9520	cover	%	13	0.81	1.373	1-80
Rhytidiadelphus loreus	biom	0.4195	1.0209	ln cov	%	29	0.87	0.233	1-90

[a]Biomass is predicted in grams from least squares estimates of plant biomass from measurements of plant dimensions. Log transformations (natural log) were used when they significantly improved coefficient of determination and decreased mean square error. The model used is indicated in column 5 (X_i). Equations give biomass in grams per shoot or, for regressions based on percentage of ground cover, grams per square meter.

[b]Prod = annual twigs and foliage, wood = woody biomass (not including annual twigs), twig = annual twigs, fol = leaf blades and petioles, biom = total aboveground biomass.

[c]ln dia = $\log_e$ of basal shoot diameter, ln cov = $\log_e$ percentage of projected ground cover, ln len = $\log_e$ of shoot or final length, ln rad = $\log_e$ radius of fragment size, cover^2 = (percent ground cover on 0.1 − m^2 plot)^2.

[d]Source: Ward Brady, Arizona State University, unpublished data.

[e]Either herb shoot-length or percentage of ground cover were independent variables, depending on density and vertical dimensionality of the species.

Horizontal shrubs may have a precise cover-biomass relationship. The relationship of *Vaccinium parvifolium* (red huckleberry) growing robustly on an open, sunny site is highly variable, but under a dense overstory canopy, where it is usually decumbent, the relationship is good (r^2 = 0.82, Table 3).

Basal shoot diameter was the most precise predictor of biomass for all shrub species, as found in research on shrub biomass in other forest regions (Whittaker and Woodwell 1968), Stanek and State 1978, Smith and Brand 1983). Shoot height and vigor class, significantly related to biomass when stem diameter was included in the regression equations, were omitted from the final model because of the subjectivity of measuring vigor class and the inefficiency of measuring shoot height in the field.

From 74 to 97 percent of the variation in biomass of the seven woody shrub species sampled was accounted for by basal stem diameter (Table 3). Foliar and annual twig biomass had

the most imprecise relationship and wood biomass the most precise relationship, as twig and foliage biomass often varies with short-term changes in microenvironment and with changes in shrub density.

The proportion of foliage in understory biomass and net annual productivity decreased with increasing stem diameter (Figure 2A). *Oplopanax horridum* (devil's club) and *Sambucus canadensis* (red elderberry) had the highest proportion of foliar biomass, *Vaccinium parvifolium* the lowest. *Oplopanax horridum, Sambucus canadensis* and *Rubus spectabilis* (salmonberry) occur in large canopy openings or in clearcuts where they develop large, open canopies. *Vaccinium* species and *Menziesia,* by contrast, tolerate closed canopies as well as clearcut or riparian openings, and they have lower proportions of foliar biomass (Alaback 1982a). *Menziesia ferruginea* and *Vaccinium parvifolium* are apically dominant, often exceeding 3 m and having a large proportion of woody biomass. In contrast, *Ribes laxiflorum* (trailing currant) rarely exceeds 0.5 m in height, creeping across forest openings in a prostrate life-form. The proportion of foliar biomass of these species and the rate of woody biomass accumulation are consistent with differences in life-form and autecology (Figure 2A, B) and with patterns of regression equations reported for shrub biomass in the northeastern United States (Whittaker 1966, Whittaker and Woodwell 1968).

Regression equations for woody biomass varied significantly (Table 5). A *Vaccinium parvifolium* stem 11 mm in diameter had more than 17 times the biomass of an *Oplopanax* stem of the same size (Figure 2B). The three most robust woody species had significantly different regression equations for both y-intercept and slope ($P = 0.95$ and 0.99, respectively). The most distinct difference between equations occurred in the largest stem size classes. A few species had similar equations, especially for twig and foliage production. *Oplopanax* and *Sambucus* were not significantly different at $P = 0.95$.

Herbaceous species. In contrast to woody shrub species, most herbaceous species showed a consistent relationship between percentage of ground cover and biomass and productivity ($r^2 = 0.84-0.95$, MSE < 0.15 g; Table 3). Taken as a whole, y-intercepts of herb cover-biomass equations are not significantly different ($P < 0.95$), but slopes are ($P > 0.99$) (Table 5). Several equations have negative intercepts. Separate biomass prediction equations were made from the small range of these species to improve the accuracy of estimates. Plants occupying 0-10 percent ground area were used to achieve adequate sample sizes for some equations, but the equations are most useful in the 0-5 percent range if the coefficient of determination is lower than that with the equation for the full set of data.

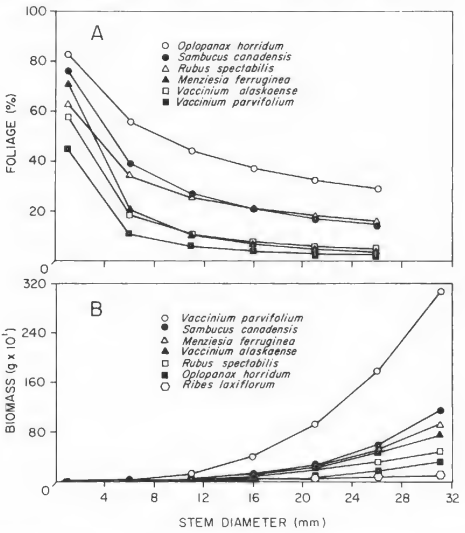

Figure 2. Relation of biomass accumulation to stem size for representative shrub species. (A) Percentage of total shrub biomass contributed by foliage is estimated from regression functions in Table 3. (B) Shrub wood biomass includes bark but not annual twigs.

Slopes of the equations were significantly different ($P = 0.95$) for all species except *Maianthemum dilatatum* (deerberry), *Coptis aspeniifolia* (gold thread), and *Moneses uniflora* (single delight), which have a similar slope but different y-intercepts. *Moneses* and *Coptis* are short (< 0.5 dm) evergreen herbs that occur primarily under continuous forest canopies. *Maianthemum* is taller (often > 0.5 dm) and occurs in more open, shoreline forests and in wetland (bog) areas.

Life-form and canopy structure were generally related to biomass. *Tiarella trifoliata* (foam flower) which accumulated the greatest biomass in relation to cover, has a vertical or multilayer (Horn 1971) life-form with short, circular leaves

interspersed along the stem. It occurs primarily in open, wet areas, especially along small streams. *Rubus pedatus,* by contrast, has a low, creeping life-form with intermittent clusters of leaves (monolayer structure) along surficial runners. It occurs in clearcuts and old-growth forests. On the average, 50 percent cover of *Tiarella* had six times the biomass of the same area of *Rubus pedatus* (Figure 3).

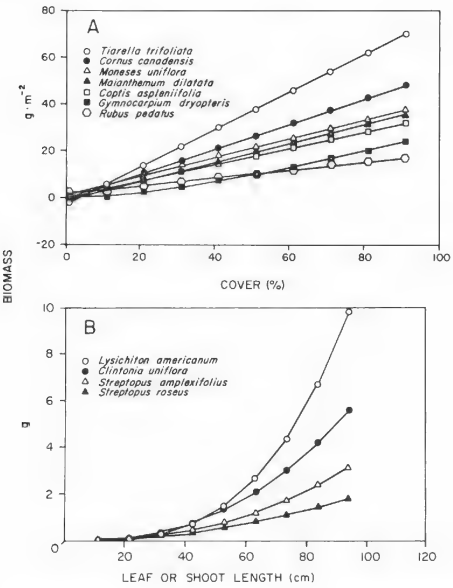

Figure 3. Relation of herb biomass to percentage of ground cover and leaf or shoot length.

Most fern and lily species (*Clintonia, Streptopus,* and *Lysichiton*) have a strong vertical component and a highly variable relationship between ground cover and biomass. Shoots of many of these species change orientation with length, from short and almost flat on the ground to large, robust, and nearly vertical. This distribution factor naturally means a less precise relationship of biomass to projected ground cover. For these species, plant shoot height (or frond length) was the best predictor (Figures 3, 4).

Regression equations for several fern and lily species were among the most precise in this study ($r^2 > 0.98$, MSE < 0.01 g). As with other herbs, the most significant difference between equations was not y-intercept, but slope. *Clintonia* and *Lysichiton* have succulent, elongate leaves very different in length (*Clintonia* usually less than 2 dm, *Lysichiton* often more than 10 dm). These species had similar biomass regression equations ($P < 0.95$ for both slope and aspect). The two species of *Streptopus,* owing to their distinct branching patterns, had significantly different slopes and y-intercepts ($P > 0.99$).

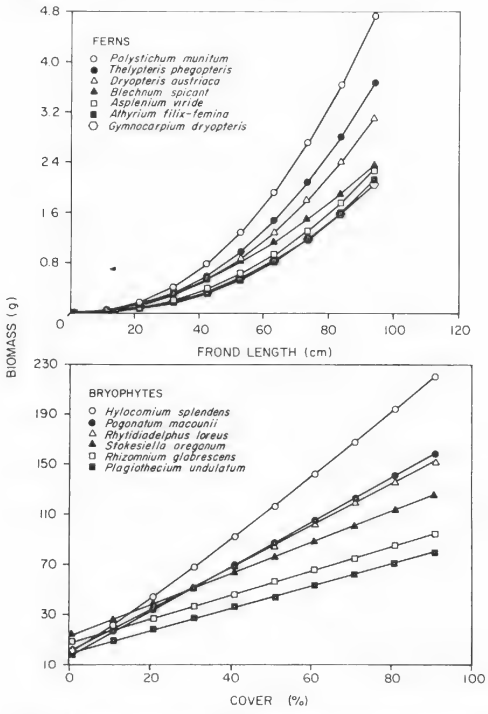

Figure 4. Relation of fern and bryophyte biomass to frond length and percentage of ground cover.

Biomass accumulation of fern species varied widely per unit frond length. *Athyrium* and *Dryopteris,* although similar in leaf morphology, had significantly different biomass equations as an *Athyrium* frond 70 cm long has less than half the biomass of a *Dryopteris* frond of the same length. But *Dryopteris* and *Gymnocarpium,* with distinctly different leaf morphology, had insignificantly different biomass equations. Both species grow under dense *Tsuga heterophylla* canopies where vascular plants are few. All regression equations differed significantly except

those for the three least dense species (*Gymnocarpium dryopteris, Athyrium filix-femina,* and *Asplenium viride*).

Bryophytes and lichens. All nine bryophytes and the one foliose lichen sampled showed consistent biomass-cover relationships (Table 3, Figure 4), those for the two feather moss species (*Hylocomium* and *Rhytidiadelphus*) and the liverwort (*Jungermannia*) being curvilinear. Dense carpets of feather mosses are generally older than small patches, a difference in age structure that may account for the nonlinear relationship (higher percentages of cover representing large, older clones), as it does in the small range of the herb-cover equations.

All but one of the groups of regression equations (for *Pogonatum macounii* and *Rhytidiadelphus loreus*) had significantly different y-intercepts (P_5 0.95). Species that tend to form thick, broad carpets under mature and old-growth forests had the greatest biomass density; shorter, sometimes solitary species (*Rhizomnium glabrescens* and *Plagiothecium undulatum*) that form small, diffuse clumps on specialized substrates like logs and stumps, had the least.

Effects of Phenology and Site

The difference between estimates of percentage of ground cover and biomass made on 29 June, 28 July, and 28 August (86.6, 87.5, and 86.2 kg ha^{-1}) is well within the margin of error of measurement. If the data are typical of the study area, most annual growth of understory vegetation occurs before 1 July. Accordingly, no significant relationship was found between the location or date of sample collection, relative to the beginning or end of the growing season, and the prediction equations (Table 4). A detailed 1-year study of the phenology of biomass and nutrients on a site in the northern end of the study area confirmed that plant ground cover or biomass changed little between 1 July and 1 September (Hanley and McKendrick 1985).

Because site was an insignificant factor in the biomass-dimension regression ($P < 0.95$; Table 4), the equations should provide reasonable estimates of biomass and productivity of plant species in environments similar to those in coastal Alaska. For relationships such as biomass to percentage of cover, additional sampling of specific habitats may yield more precise estimates (Daubenmire 1968, Payne 1974). Prediction of biomass made from frond length or shoot length of herbs and ferns tended to be the most robust among sites.

TABLE 4. Effects of site, phenology, and year of measurement on biomass regression equations of representative woody shrub, fern, and herb species.

Source of variation	Variation (%)	F Statistic
	Vaccinium alaskaense	
Size class (diameter)	69.4	629.0
Sampling site	7.9	9.0
Phenology	0.03	0.3
Year of sampling	0.2	2.0
Residual error	22.4	
	Blechnum spicant	
Size class (frond length)	88	387.0
Sampling site	2	3.0
Phenology	1	0.4
Residual error	10	
	Cornus canadensis	
Size class (cover)	76	70
Sampling site	2	0.5
Phenology	0	0
Year of sampling	0.3	0.3
Residual error	21	

Sampling Analysis

Vegetation tends to vary most in clearcuts, with patches of vigorously growing and sprouting shrubs occurring beside dense pockets of *Tsuga* or *Picea* regeneration with little understory. Typically, 15 or more $4-m^2$ plots or 60 or more $1-m^2$ plots are needed for a precise estimate of total understory biomass (Figure 5). The same precision in mature forests may require only 10 to 15 $4-m^2$ plots or 30 to 40 $1-m^2$ plots, yet may yield more accurate estimates because of depauperate vegetation. Most understory species in mature forests are bryophytes and herbs, usually growing at low densities. Only 8 to 10 $4-m^2$ plots were needed for precise estimates under old-growth biomass (Figure 5), which had substantially more vegetation than the mature stage and less variation than the clearcut stage.

If we assume that each $1-m^2$ or $4-m^2$ plot represents an independent estimate of understory biomass for a given stand, and that errors in estimates are normally distributed, the number

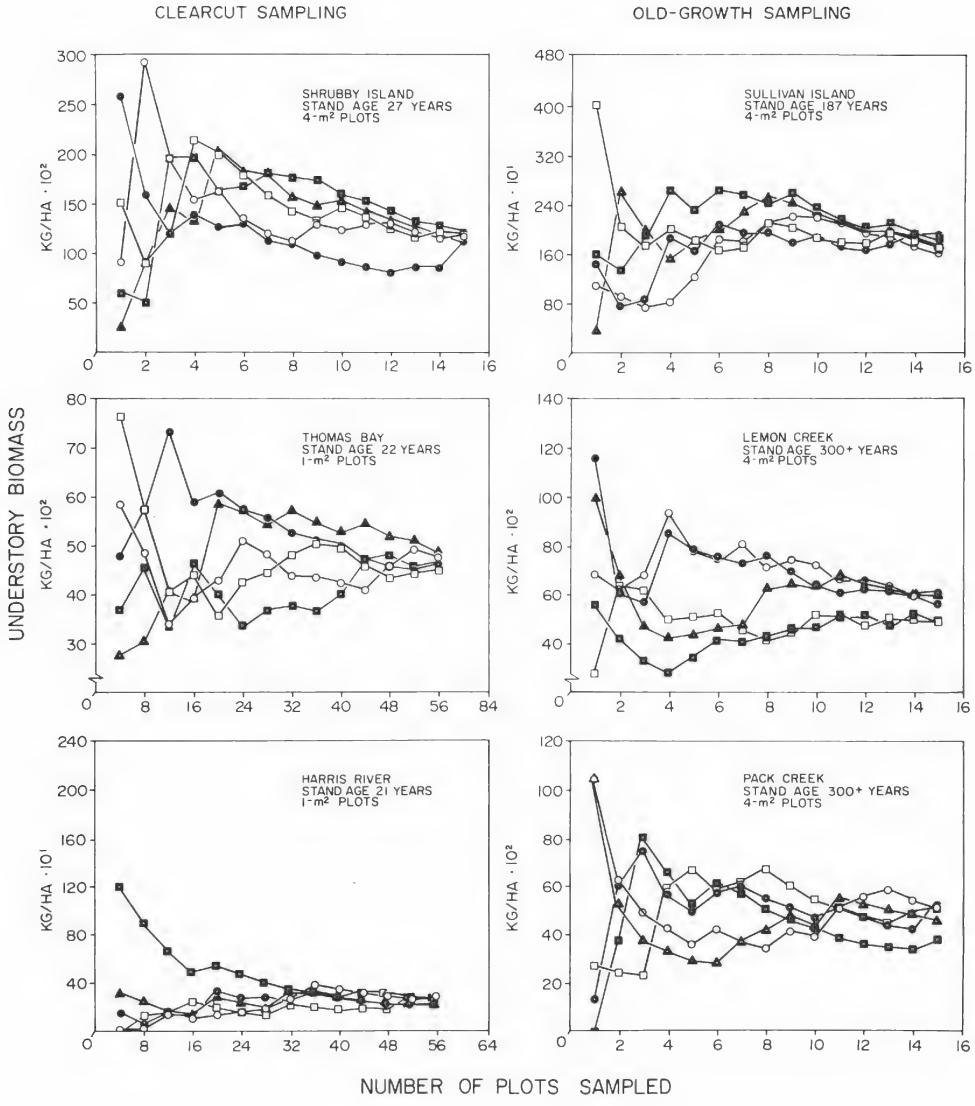

Figure 5. Sampling-area curves for biomass estimation on clearcut and old-growth plots. Five separate runs for each site illustrate the effect on biomass estimates of randomly choosing plots in different sequences.

TABLE 5. Comparison of slopes and intercepts of biomass equations for different species derived from full and reduced regression models.

Biomass component Species being compared	df‡	F̂ intercepts	F̂ slopes
Woody biomass			
Rubus spectabilis, Menziesia ferruginea	4/60	3.47*	
	3/62		0.10
Vaccinium parvifolium, Menziesia ferruginea	4/42	5.13**	
	3/43		11.21**
Vaccinium alaskaense, Ribes laxiflorum	4/71	2.79**	
	3/43		0.70
Vaccinium alaskaense, Rubus spectabilis	4/102	0.03	
	3/103		3.34*
Twig and foliage			
Menziesia ferruginea, Ribes laxiflorum, Rubus spectabilis,	10/257	0.80	
Vaccinium alaskaense, V. parvifolium	6/261		34.73**
Vaccinium parvifolium, Menziesia ferruginea	4/41	2.37	
	3/42		0.88
Menziesia ferruginea, Vaccinium alaskaense	4/181	2.20	
	3/182		0.30
Rubus spectabilis, Ribes laxiflorum	4/55	0.57	
	3/56		8.34**
Rubus spectabilis, Vaccinium alaskaense	4/216	0.57	
	3/217		0.68
Shoot length			
Streptopus roseus, S. amplexifolius, Clintonia	8/77	1.13	
uniflora, Lysichiton americanum	5/80		4.08**
Clintonia uniflora, Lysichiton americanum	4/41	0.32	
	3/42		2.05
Streptopus amplexifolius, S. roseus	4.36	6.46**	
	3/37		6.76**
Clintonia uniflora, Streptopus amplexifolius	4/29	0.06	
	3/30		9.16**
Percentage cover			
Cornus canadensis, Coptis aspleniifolia, Tiarella trifoliata	6/60	0.07	
	4/62		6.70**
Cornus canadensis, Tiarella trifoliata	4/43	0.02	
	3/44		6.61**
Coptis aspleniifolia, Rubus pedatus	4/37	2.12	
	3/38		28.54**
Rubus pedatus, Tiarella trifoliata	4/40	0.40	
	3/41		32.51**
Cornus canadensis, Maianthemum dilatata	4/36	0.29	
	3/37		5.27**
Maianthemum dilatata, Coptis aspleniifolia	4/30	3.82*	
	3/31		0.03
Cornus canadensis, Rubus pedatus, Tiarella trifoliata	6/63	0.39	
	4/65		22.69**

* Significant at P = .095
** Significant at P = 0.99
‡ Degrees of freedom; number of parameters in model/number of observations

of samples for a given level of precision can be estimated from sample variance (Cochran 1963). Estimates are inflated because of the nonrandom distribution of forest vegetation, but still provide a useful index of sampling requirements for various sites.

A strong pattern of change in sampling requirements with stand age is suggested by the variance estimates for 60 stands studied. For the same level of precision, recently logged sites require more plots, by 2 or more orders of magnitude, than mature or old-growth forests. In general, understory biomass varies in proportion to accumulated understory biomass ($r = 0.70$, $P > 0.99$).

Vegetation structure should be considered before assessing how best to estimate biomass by means of regression equations. Forest understory vegetation in coastal Alaska is patchy and nonrandom in distribution, as in other forest regions (Kershaw 1963); therefore, plot size and sampling intensity have important bearing on the adequacy of the sample (Kershaw 1963, 1973; Daubenmire 1968).

The effect of plot size on biomass estimation of coastal Alaskan vegetation has been evaluated on $0.1-m^2$, $1-m^2$, and $4-m^2$ plots. The $0.1-m^2$ plots recommended by Daubenmire (1959) are ideal for herb and moss biomass, quick to measure and reasonably precise for estimates of percentage of ground cover when 30 to 40 are located on a site. Species with coarse-grained spatial patterning, like woody shrubs, have lower variance on $1-m^2$ plots. For herbs, $4-m^2$ plots give less variance than $1-m^2$ plots but require more time for similar precision. The $4-m^2$ plots are most accurate and field efficient for clumps of large woody shrubs such as *Menziesia ferruginea* or *Vaccinium alaskaense*. Overall, $4-m^2$ plots were the most efficient for estimating understory biomass. In recently clearcut sites, 2.6 times more $1-m^2$ than $4-m^2$ plots are needed for measuring biomass to within 10 percent of the mean, yet 30 $1-m^2$ plots may take twice as much time to measure as 10 $4-m^2$ plots. This ratio is maintained or exceeded with older age classes. If highly precise measurements of large woody shrubs are required, even larger plots may be needed.

Discussion

The tendency for complex, multilayered canopies to accumulate the most biomass and for prostrate monolayer species to have modest accumulation per unit area or stem diameter holds between and within life forms. Tolerance of species to low-level solar radiation is also related to biomass. Herbs growing under dense overstory canopies (i.e. *Moneses uniflora, Gymnocarpium dryopteris*) have the least biomass, woody shrubs growing in early seres, as in the riparian zone or in recent clearcuts, have the most biomass (*Rubus spectabilis, Sambucus canadensis*).

Even if appropriate equations are selected for a given species, other sources of error may compromise the precision of estimates. In nondestructive sampling, the principal sources are: 1) application of an equation to plants in a different phenological stage than that of the plants used to develop it, 2) differences between microenvironments or the genetics of samples used to develop the equation and of plants to which it is applied, and 3) inadequate or biased sampling design.

The first two sources of error may be easily evaluated for equations developed in this study. Plot data taken in southeast Alaska between 1 July and 1 September at sea level (or equivalent dates at higher elevations) should be within the range of samples used to develop the regression equations. The biomass equations are most likely to apply to data taken within the coastal Alaska *Picea sitchensis-Tsuga heterophylla* forest region. Equations for plants invading recently disturbed sites have the greatest potential for error, as clearcuts less than 10 years old and primary successional sites with robust shrub and herb growth were not sampled as thoroughly as other age classes.

Understory species colonize and expand, decay and become extinct over the life of a forest stand (Alaback 1982a, 1982b). When the overstory canopy opens after windthrow, for example, or when it becomes more dense after canopy closure, leaf area and twig production change first. Eventually the distribution and density of shoot size classes within a clone change, through new sprouts or the death of old shoots (Tappeiner 1971, White 1979). Shrub biomass samples for this study were primarily collected from vigorous plants in clearcut or old-growth

areas; therefore, if the equations are used for shrubs dying back under a rapidly closing canopy, overestimates may result. Conversely, foliar biomass and productivity of unusually vigorous shrubs growing in recently disturbed sites may be underestimated.

The advantage in using cover-based biomass equations for shrubs is that many cover estimates can be made in the time required for a few measurements of basal shoot diameter or canopy volume. In recently clearcut vegetation, measurement of shrub shoot diameter commonly took 10- to 15-fold the time required to make estimates of percentage of cover. Separate biomass-cover regression equations are needed for each sere and site if biomass estimates are to be accurate.

The third source of error, the size of nondestructive samples for estimating understory vegetation biomass, has been given little attention despite its importance. Biomass often has an exponential relationship to plant abundance, so that more plots are needed for estimating biomass than are needed for estimating frequency or cover. During the first year of a study of forest succession in southeast Alaska, 40 to 60 $1-m^2$ plots were sampled in each stand (Alaback 1982a, 1982b), but 10 to 15 $4-m^2$ plots, more field efficient and yielding similar precision, were used in the last 2 years of the study.

In clearcuts or other recently disturbed areas where vegetation tends to be patchy, other sampling schemes may be necessary; 100 or more plots may be needed for achieving the same accuracy that 20 to 30 plots yield in mature or old-growth forests. Double sampling may be more efficient than single-stage plot sampling on highly variable sites. For example, percentage of ground cover could be measured on a large set of plots, and a subset could be measured for basal diameters of shrubs or trees and shoot lengths of ferns or herbs. A relationship between stem and shoot data and percentage of ground cover could then be developed so that biomass could be estimated for all plots (Cochran 1963, Pieper 1978).

Applicability of the biomass equations in this study to regions outside southeast Alaska is unknown. Many of the species extend into northern California, others (especially bryophytes) into interior Alaska and northern Canada. The relationships may differ in these locations because the continental climates and geochemistry contrast strongly with the cool, wet, maritime climate and the complex geology of southeast Alaska (Andersen 1955). Further research is necessary for assessing the structure and performance of the species along environmental gradients.

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Distributions of 40 Rare Vascular Plants in the Alatna River Drainage of the Central Brooks Range, Alaska

Abstract

Forty rare plants were collected beyond their known distribution ranges on the south slope of the Brooks Range given by Hulten (1968). Twenty-two of the 40 species distributions suggest northward post-Pleistocene migration from southern refugia. The habitat preference of *Campanula aurita* and *Cypripedium calceolus* subsp. *parviflorum* for dry south-facing limestone outcrops suggests possible survival as part of the Pleistocene steppe tundra flora.

Introduction

Remote regions of Alaska are receiving more scientific attention which is bridging gaps in species distribution knowledge. Species reported here are important because they were collected beyond the range given by Hulten (1968). They add to recent range extensions for other parts of Alaska (Kelso 1983, Phillips 1983).

Glacial events and vegetation refugia influence the present distribution patterns in the Alatna River drainage. Post-Pleistocene vascular plant migrations into and within the region are dynamic, emphasizing the requirement of contemporary floristic surveys for detailed distribution mapping and phytogeographical interpretation.

The Alatna drainage has received little botanical attention until recently because it has been accessible only by foot, small boat, and aircraft. In recent years access to the area has improved considerably. Jordal (1951) completed a floristic collection along the southern portion of the drainage. Murray (1978) collected around the confluence of the Nahtuk Creek and the Alatna River, and at the Alatna headwaters, and is compiling a summary of the floristic records of the last ten years for the state of Alaska. Cooper (1983) collected in the alpine area of the Arrigetch headwaters.

Collection Area

The Alatna drainage (67°30'N, 154°W) is situated in the newly designated Gates of the Arctic National Park. It transects the northern latitude white spruce, *Picea glauca* (Moench) Voss, forest-tundra ecotone. The area is covered by the Survey Pass Quadrangle of the U.S. Geographic Society topographic map series (scale 1:250,000). The upper drainage is approximately 90 km wide and 150 km long with bedrock types of granite, metasedimentary limestones, and unmetamorphosed shales and sandstones (Nelson and Grybeck 1980, 1981). Small cirque glaciers in the South Arrigetch, Arrigetch, Awlinyak, and Unakserak Creek Valleys survive the three major glacial advances which occurred in the southern Brooks Range (Hamilton 1966, 1981, 1982). The climatic regime follows a maritime (west) to continental (east) gradient across the drainage (U.S. Environmental Data Service 1977).

Methods

Plants were collected in the drainage during the summers of 1978, 1981, and 1982. Species occurrences were recorded for the eight main tributaries of the upper Alatna drainage (Figure 1). Specimens were verified by Ron Hartman of the University of Wyoming and David Murray of the University of Alaska. The *Antennaria* species were verified and retained by Ledyard Stebbins of the University of California, Davis. Other voucher specimens are deposited at the RM herbarium in Laramie, Wyoming.

Results

Of the 282 species collected in the Alatna River drainage 40 are range extensions (Table 1). Reported species were found beyond the solid lines and in gaps within the predicted ranges (cf. Hulten 1968). The fact that 14 percent of the

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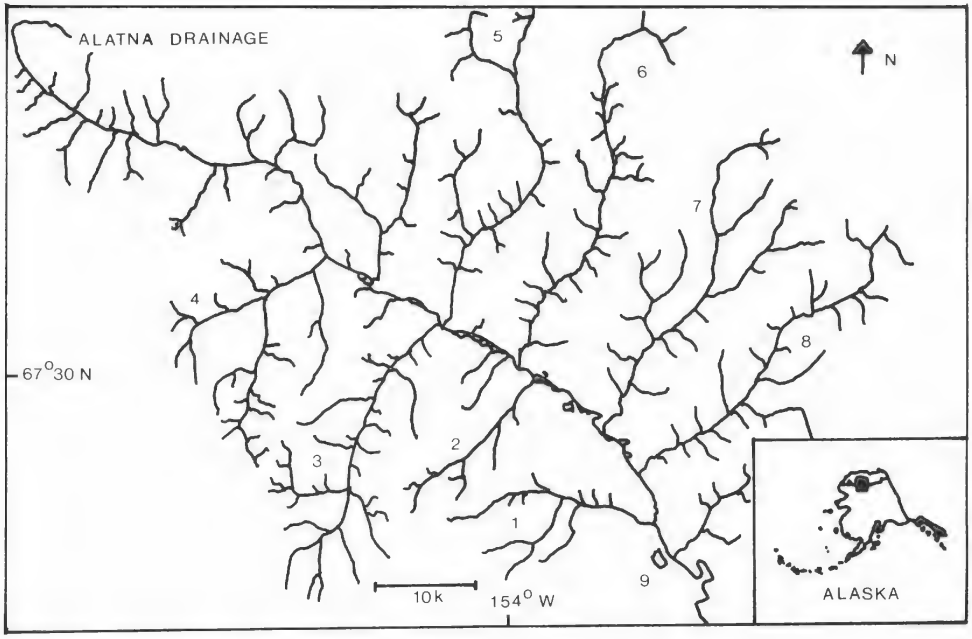

Figure 1. Location of the collection sites within the Alatna River drainage on the south slope of the Brooks Range. The insert shows the position of the Alatna drainage on the latitudinal boundary between the forest and tundra vegetation. The valley sites are: 1—South Arrigetch (67° 26N, 153° 58W), 2—Arrigetch (67° 27N, 154° 05W), 3—Awlinyak (67° 24N, 154° 40W), 4—Akabluak (67° 33N, 154° 40W), 5— Unakserak (67° 46N, 154°W), 6—Kutuk (67° 44N, 153° 48W), 7—Pingaluk (67° 40N, 153° 30W), 8—Nahtuk (67° 34N, 153° 14W), and 9—along the Alatna River (66° 30N-67° 38N, 153° 15W-154° 30W).

collected flora were found beyond the recorded distribution demonstrates the great potential for finding range extensions in this part of Alaska. A complete list of the 282 species and collection localities is given in Odasz (1983).

Distributions of 22 of the 40 plants show a similar pattern. Their main distribution is south of the Brooks Range. Eleven of these are species limited to North America, 2 are amphi-Pacific, 2 are amphi-Atlantic and 6 are circumpolar plants. The rest of the species have wider distributions in Alaska, occurring in the alpine or on both sides of the Brooks Range.

Discussion

At the higher latitudes, following ice recession, plants moved north and west in Norway (Hulten 1971, Wright 1977) and in Alaska (Hopkins *et al.* 1981). The northward expansion of conifers and associated species in the Alatna drainage, after deglaciation 10,800 years ago (Hamilton 1982), is supported by recent vegetation (Odasz 1983), palynological (Brubaker *et al.* 1983), pedogenic (Ugolini *et al.* 1981) and radiocarbon (Hamilton and Brubaker 1982, Hopkins *et al.* 1981) data which corroborate earlier observations (Griggs 1934, Marshall 1970).

Such a northward route may have been followed by herbaceous species from ice-free refugia. Plants with main distributions south of the Brooks Range penetrate the altitudinal boundary of the range in favorable sites along drainages. Good examples include: *Mertensia paniculata* var. *paniculata, Amerorchis rotundifolia, Campanula rotundifolia,* and *Cypripedium calceolus* subsp. *parviflorum.*

Mertensia paniculata is abundant in moist, shaded treelimit stands and on gravel bars in only the Awlinyak site and one other site 25 km south of the Awlinyak-Alatna Rivers confluence.

TABLE 1. Rare species and range extensions. Nomenclature follows Hulten (1968). For a detailed description of habitat and location see Odasz (1983).

Lycopodiaceae
Lycopodium alpinum
Lycopodium complanatum

Aspidiaceae
Dryopteris dilatata subsp. *americana*

Juncaginaceae
Triglochin palustris

Cyperaceae
Carex aurea
Carex concinna
Carex krausei

Orchidaceae
Cypripedium calceolus subsp. *parviflorum*
Amerorchis rotundifolia
Listera borealis

Betulaceae
Betula papyrifera subsp. *humilis*

Ranunculaceae
Ranunculus gelidus subsp. *grayi*

Brassicaceae
Draba cana
Draba longipes
Parrya nudicaulis

Saxifragaceae
Saxifraga oppositifolia subsp. *smalliana*
Saxifraga flagellaris subsp. *setigera*
Saxifraga spicata
Saxifraga nivalis

Rosaceae
Rubus arcticus subsp. *acaulis*
Potentilla biflora
Potentilla virgulata
Geum glaciale
Dryas drummondii

Fabaceae
Astragalus nutzotinensis
Oxytropis campestris subsp. *jordalii*
Oxytropis deflexa var. *foliolosa*
Oxytropis koyukukensis

Pyrolaceae
Moneses uniflora

Ericaceae
Ledum palustre subsp. *groenlandicum*
Oxycoccus microcarpus

Gentianaceae
Gentiana propinqua subsp. *propinqua*

Boraginaceae
Mertensia paniculata var. *paniculata*

Scrophulariaceae
Castilleja pallida subsp. *elegans*

Campanulaceae
Campanula aurita

Asteraceae
Erigeron acris var. *elatus*
Antennaria monocephala subsp. *monocephala*
Antennaria isolepis
Crepis elegans

According to Hulten (1968) this boreal species is limited to woods and riverbanks and covered an extensive area to the south before the maximum Wisconsin glaciation. Subsequently it expanded into the ice free areas (Hulten 1937). *Amerorchis rotundifolia* was found only on the moist hummocks close to Kutuk Lake. It has a similar history to *M. paniculata* (Hulten 1937).

Campanula aurita and *Cypripedium calceolus* subsp. *parviflorum* were found on steep south-facing limestone bluffs above the Alatna River. The *Cypripedium* subspecies was found to the south along the Bettles River by Harmes in 1973 and may occur along the limestone belt of the southern Brooks Range (Murray personal communication). The present distribution and ability of these two species to persist in cold, xeric sites suggest their possible survival in the Pleistocene steppe tundra vegetation.

The *Antennaria isolepis* collection bridges the wide distribution gap from the Yukon River to the Colville River on the Arctic slope.

Exotic and weedy species are also expected to invade the Alatna drainage of the Gates of the Arctic National Park. Visitation from surrounding settlements, airports and regions outside of Alaska increases the potential for species introduction. (Hence: check your cuffs!)

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Brood Habitat of Merriam's Turkeys in South-Central Washington

Abstract

Merriam's wild turkey (*Meleagris gallopavo merriami*) brood habitat use was studied from 17 May to 6 July 1981 in Klickitat County, south-central Washington. Garry oak (*Quercus garryana*) and ponderosa pine (*Pinus ponderosa*) -Garry oak habitats were used extensively by broods, and Douglas-fir (*Pseudotsuga menziesii*) and non-forest habitats were used less than expected ($P < 0.05$). Broods used areas with greater canopy cover, lower visibility, less slope, lower understory coverage, and habitats closer to cover than the overall environment.

Introduction

Merriam's turkeys were introduced in south-central Washington in 1960. While turkeys are currently managed as a game species in Washington, data concerning their habitat use are lacking.

Pack *et al.* (1980) statistically analyzed characteristics of turkey brood habitat in West Virginia; however, quantitative analyses of brood habitat use by Merriam's turkeys are not available. Healy and Nenno (1983) emphasized the importance of managing turkey habitat for young broods. The objectives of this study were to: 1) statistically evaluate turkey brood habitat in south-central Washington, and 2) provide data useful for management of brood habitat.

Study Area

The 4290 ha study area was located in southern Klickitat County, Washington, approximately 6 km northeast of the Klickitat River mouth. The area was characterized by gently undulating terrain dissected by steep canyons. Elevations ranged from 120 to 550 m above mean sea level. Seventy-four percent of the study area was forested. Forest types were described as Garry oak, ponderosa pine, and Douglas-fir by Franklin and Dyrness (1973). Nonforested areas were rangeland, wheat fields, and alfalfa pastures. Primary land uses were cattle grazing, wheat farming, and timber production.

Methods

Turkeys were trapped during winter using rocket nets or panel traps. Transmitters (87 g; Telonics, Mesa, Arizona) were attached to hens by a backpack mount with the harness under each wing (Everett *et al.* 1978). Radio-locations were determined by triangulation using a three-element hand-held yagi antenna and standard compass. A minimum of three bearings were taken for each location using the "loudest signal method" (Springer 1979).

Habitat use by four radio-marked broods was sampled from 17 May to 6 July 1981. Data were collected from 1-22 days post-hatching because most poult mortality occurs during this time (Glidden and Austin 1975, Little and Varland 1981) and brood food habits and habitat use may change as broods grow older (Williams *et al.* 1973, Healy *et al.* 1975, Nenno and Lindzey 1979, Pack *et al.* 1980). Each brood was located twice every other day. Locations were separated by a minimum of three hours and alternated between diurnal time periods: (1) sunrise to 1000 hours, (2) 1000 hours to 1400 hours, and (3) 1400 hours to sunset.

The northwest corner of a 15 x 25 m plot (Daubenmire and Daubenmire 1968) was placed at brood locations, and the plot was used to sample canopy height, height to lowest live tree limb, tree basal area, canopy coverage, distances to nearest cover and clearing, understory height, understory coverage, slope, and visibility. Mean canopy height and height to lowest live tree limb were determined from measurements taken with an Abney level on a subjectively selected "average" tree within the stand. Tree basal areas were calculated from diameter at breast height and density data (Avery 1967:40). Percent canopy coverage was obtained by averaging readings taken at each plot corner using a convex spherical densiometer (Lemmon 1956). Distances to nearest

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cover and clearing greater than 1 ha in size were measured from aerial photographs. Understory height was determined from an ocular estimate of the mean height of all shrub, forb, and grass species within the plot. Understory coverage was calculated as the sum of the estimated percent coverage of shrubs, forbs, and grasses within the plot. Percent slope was measured with an Abney level. Visibility was considered an index of cover density and sampled by modification of ocular estimation (DeVos and Mosby 1969:140); visibility was estimated from the plot center as the distance of unobstructed sight, averaged among four cardinal directions, approximately 1 m above and parallel to the ground. Fifty-five control plots were randomly selected for sampling from systematically located points over the entire study area. Control plots were the same size, and habitat variables were sampled in the same manner as brood plots. Control plots were used analytically to represent the random environment.

Each brood and control plot was classified as one of four habitat types based on ocular estimation of canopy coverage by tree species: 1) Garry oak = $\geq$ 60 percent Garry oak cover with $<$ 10 percent ponderosa pine and/or 30 percent Douglas-fir coverage; 2) ponderosa pine-Garry oak = $\geq$ 10 percent ponderosa pine coverage, 5–90 percent Garry oak cover, and $<$ 30 percent Douglas-fir cover; 3) Douglas-fir = $\geq$ 30 percent Douglas-fir coverage; and 4) non-forest = $<$ 5 percent total tree coverage in an area larger than 1 ha. Detailed information concerning these habitat types is reported by Mackey (1982).

Multivariate analysis of variance (MANOVA) (Cooley and Lohnes 1971:223) was used to test the hypothesis of no difference between brood and control plots considering all 10 physiographic characteristics simultaneously. If differences were detected, tests were conducted to determine which physiographic characteristics contributed significantly to the difference. Chi-square goodness-of-fit analysis was used to test the hypothesis that habitat types were utilized randomly (Sokal and Rohlf 1969:552). If a chi-square test was significant, methods of Neu *et al.* (1974) were used to determine which habitat types were used more or less than expected. "Expected" refers to the expected proportion of observations under the null hypothesis of use in proportion to availability. Expected values for chi-square tests were calculated from proportions of each habitat within the study area. Brood plots were considered independent samples of brood habitat use on the study area. Tests were considered significant at $P < 0.05$.

Results

Broods remained separate from each other during the study period and were dispersed over the entire study area. Chi-square goodness-of-fit analysis indicated habitat use was not random ($P < 0.005$, $\chi^2 = 32.1$, $df = 3$). Garry oak and ponderosa pine-Garry oak habitats were used more than expected; Douglas-fir and non-forest habitats were used less than expected (Table 1).

MANOVA analysis indicated a difference ($F_{(10,103)} = 4.33$, $P = 0.001$) between brood and control plots. Percent slope and understory coverage were less at brood plots than control plots ($P = 0.001$) (Table 2). Canopy cover was greater at brood plots, and brood plots were closer to cover than control plots ($P = 0.006$). Visibility was lower at brood plots ($P = 0.004$). Understory height was lower at brood plots, a difference which approached significance ($P = 0.056$). These data may be conservative since an unknown number of random control plots may have been sampled in suitable brood habitat.

Discussion

Garry oak and ponderosa pine-Garry oak habitats were heavily used, and non-forest habitat was used very little by turkey broods. These data indicate the importance of forest cover to young turkey broods. Studies have noted the preference of forest clearings or forest/non-forest edges to turkey broods in some eastern states (Hillestad and Speake 1970, Speake *et al.* 1975, Pack *et al.* 1980, Healy and Nenno 1983). This is likely due to greater insect and understory vegetation availability in clearings than in eastern hardwood forests (Blackburn *et al.* 1975, Martin and McGinnes 1975, Healy and Nenno 1983). Healy and Nenno (1983) identified the occurrence of herbaceous vegetation as the "essential feature" of turkey brood habitat. On my study area, Garry oak and ponderosa pine-Garry oak forests were characterized by diverse understory vegetation (Mackey 1982), and commonly contained clearings less than 1 ha in size. There appeared to be an abundant supply of insects and herbaceous vegetation in these habitats that likely provided broods with an adequate food supply and escape cover. Williams

TABLE 1. Analysis of wild turkey brood habitat use Klickitat County, Washington, 1981.

Habitat Type	Locations Observed	Proportion of Observations	Proportion of Study Area	95% Family Confidence Interval on Proportion of Observations	Use Category[1]
Garry oak	42	0.67	0.48	$0.52 \leq P_1 \leq 0.82$	M
Ponderosa pine/Garry oak	19	0.30	0.15	$0.16 \leq P_2 \leq 0.44$	M
Douglas-fir	1	0.02	0.11	$0.00 \leq P_3 \leq 0.06$	L
Non-forest	1	0.02	0.26	$0.00 \leq P_4 \leq 0.06$	L
Total	63	1.01	1.00		

[1]M = habitat used more than expected; L = habitat used less than expected ($P < 0.05$; adjusted $Z = 2.5$)

TABLE 2. Physiographic characteristics of wild turkey brood (N = 59) and control (N = 55) plots, Klickitat County, Washington, 1981.

Physiographic Characteristics	Brood Plots		Control Plots		Calculated F – Value	P > F
	$\bar{X}$	SD	$\bar{X}$	SD		
Slope (%)	15.6	10.1	23.7	16.1	10.60[a]	0.001
Understory coverage (%)	33.5	14.1	47.9	25.8	13.93[a]	0.001
Canopy coverage (%)	56.5	16.0	44.9	27.6	7.71[a]	0.006
Distance to cover (m)	1.1	6.8	7.8	17.0	7.85[a]	0.006
Visibility (m)	32.7	14.2	121.0	233.2	8.44[a]	0.004
Understory height (cm)	44.0	9.5	50.5	24.1	3.72	0.056
Height to lowest live tree limb (m)	3.0	1.4	3.3	3.4	0.24	0.624
Distance to clearing (m)	129.7	180.1	139.8	214.5	0.07	0.786
Canopy height (m)	9.8	4.2	10.1	8.8	0.05	0.822
Tree basal area (m^2/ha)	21.4	15.2	16.6	15.5	2.73	0.101

[a]Brood plots and control plots are significantly different ($F_{.05}(1,112) = 3.92$).

et al. (1974) noted that turkeys will remain in or near forest cover if preferred food such as grasses and forbs are available.

Use of Douglas-fir habitat was low, possibly due to steep slopes and understory vegetation characteristic of these sites. Broods used areas with relatively gentle slopes ($\bar{X}$ = 16 percent, SD = 10) and moderate understory coverage ($\bar{X}$ = 33 percent, SD = 14). Douglas-fir habitat occurred exclusively on steep north slopes. Approximately 45 percent of this habitat had been logged within the past 20 years, creating extremely dense understory vegetation which may have restricted brood use by limiting brood mobility and/or reducing visibility of the hen for detection of predators. Pack *et al.* (1980) observed young broods preferred gentle slopes (5-15 percent), and avoided steep slopes (> 49 percent) and forests with dense woody understories.

Land uses on the study area that should be addressed by turkey habitat management programs include: 1) clear-cutting of Garry oak and ponderosa pine-Garry oak forests, and 2) increasing human development. Clear-cutting of

forests on the study area should be avoided in favor of a selective cutting method which would maintain some forest cover. If clear-cutting must occur, clear-cuts should be less than 0.5 ha in size. Construction of buildings should be restricted to non-forested areas greater than 1 ha in size to avoid destruction of brood habitat and to minimize brood disturbance.

Due to the small number of turkey broods (n = 4) considered in the analyses, results from statistical analyses in this paper should be interpreted with caution. High error rates may occur if certain statistical analyses are applied to habitat use data when sample sizes are small (J. R. Alldredge and J. T. Ratti, unpublished data). I attempted to take a conservative approach when drawing conclusions from these data. Recommendations concerning brood habitat management should not be applied outside of the study area.

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Utilization of the Columbia River Estuary by Subyearling Chinook Salmon

Abstract

Subyearling chinook salmon (*Oncorhynchus tshawytscha*) were sampled in various habitats of the Columbia River estuary (Oregon and Washington) for 18 consecutive months in 1980 and 1981. Although present throughout the year, they were most numerous from May through September. Subyearlings captured in pelagic habitats from May through August were significantly larger than those collected in intertidal areas. The diet of subyearling chinook salmon included a variety of food, primarily invertebrates. The amphipod *Corophium salmonis* was an important prey; other important prey included *Daphnia* spp. and adult dipterans. Generally, subyearlings fed more intensively in intertidal areas than in pelagic areas.

Introduction

Various investigators (Reimers 1973, Healey 1980, Kjelson *et al.* 1982, Levy and Northcote 1982, Myers and Horton 1982) have observed that estuaries are important rearing areas for some subyearling chinook salmon (*Oncorhynchus tshawytscha*). The Columbia River estuary, the largest estuary in Washington and Oregon, contains millions of subyearling chinook salmon during the spring and summer. Adult returns from these juveniles make the Columbia River system an important producer of chinook salmon; in 1979 the estimated minimum run of fall chinook salmon was 355,500 adults (Bohn and Stockley 1981). Although subyearling chinook salmon are an important part of the fish community of the Columbia River estuary, little has been published about their use of the estuary. McCabe *et al.* (1983) described relationships between juvenile chinook salmon and other fish species in the Columbia River estuary, but important specific information on subyearling chinook salmon was not presented.

The purpose of this paper is to provide information on the utilization of the estuary by subyearling chinook salmon. Specific objectives include determinations of (1) primary habitats utilized, (2) spatial and temporal distributions, (3) size characteristics, and (4) feeding habits, including comparisons of feeding intensities in different habitats.

Methods

Sampling

Bottom trawls, purse seines, beach seines, and trapnets were used to sample various habitats of the estuary. An 8 m semiballoon shrimp trawl was used in benthic areas of channels. Trawl mesh size was 38.1 mm, and a liner of knotless 12.7 mm mesh was inserted in the cod end. Mesh size for all gear types is given as stretched size. The trawl was towed for five minutes, generally upstream during flood tide. Pelagic areas were sampled with a 200 x 9.8 m variable mesh purse seine; mesh sizes were 19.0 mm and 12.7 mm. The bunts of the purse and beach seines were constructed of knotless mesh to reduce scaling of fish. The purse seine was set upstream for five minutes during various tide stages. Intertidal areas (and often adjacent subtidal regions) were sampled with two 50 m variable mesh beach seines. Although both nets had the same mesh sizes (19.0, 12.7, and 9.5 mm), one was 4.0 m deep at its deepest point, whereas the other was 3.4 m. We beach seined during various tidal stages, using a method similar to that of Sims and Johnsen (1974). Collapsible trapnets were used to sample fish in tributaries, sloughs, and coves. The trapnet leads were 15.2 m long by 0.9 m high and were attached to an object on or near the shoreline. Mesh size in the leads was either 44.4 mm or 19.0 mm. The body of the net was 4.9 m long and constructed of 19.0 mm mesh netting. Trapnets were fished for about 24 hours per set.

The estuary was divided into upper and lower zones (Figure 1); the two zones were then subdivided into pelagic and intertidal habitats. In the upper estuary, pelagic and intertidal areas were considered fresh water, whereas in the lower estuary these habitats were classified as mixed. Salinity in the lower estuary varies widely, depending on tidal stage and river flow, and in some places may exceed 30 ppt during flood

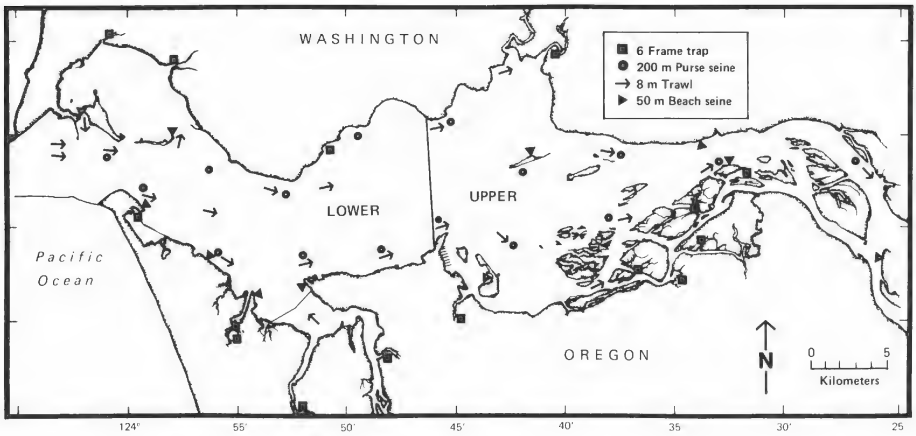

Figure 1. Locations of 63 stations in the Columbia River estuary sampled monthly from February 1980 through July 1981.

tide. Usually there is a vertical salinity gradient in the lower estuary, with highest salinity near the bottom. Saline water enters at times along the bottoms of channels in the upper estuary; however, the pelagic and intertidal sampling was generally conducted in fresh water.

Sampling was done monthly from February 1980 through July 1981; each month's effort consisted of 22 trawls, 16 purse seine sets, 11 beach seine sets, and 14 trapnet sets (Figure 1). Eleven to sixteen days were required to complete monthly sampling, depending on weather, tidal conditions, catches, and available personnel and boats. Before each set, water temperature and salinity were measured with a Beckman Model RS5-3 salinometer and probe (Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA).

Processing of Fish

Juvenile chinook salmon were measured to the nearest mm (fork length). Subyearling chinook salmon were separated from yearling chinook salmon using length-frequency histograms. When more than 50 subyearlings were caught in a set, a sample of 50 was taken and the remaining fish were counted and weighed as a group.

Five individuals from each set were kept for stomach analysis. These fish were injected with 8 percent buffered formaldehyde solution soon after capture to preserve stomach contents (Emmett *et al.* 1982). In the laboratory we removed the stomachs and placed them in individual labeled vials containing 70 percent ethanol. Food organisms were identified to the lowest practical taxon with the aid of a 10X binocular dissecting microscope, blotted, air-dried for 10 minutes, and weighed to the nearest 0.0001 g.

Food Data Analysis

Two equations were used to evaluate the food habits of juvenile chinook salmon. The importance of a prey item was assessed using a modification of the Index of Relative Importance described by Pinkas *et al.* (1971);

$$IRI = (N + W) F,$$

where

IRI = Index of Relative Importance of a prey item,
N = percent number of a prey item,
W = percent weight of a prey item, and
F = percent frequency of occurrence of a prey item.

IRI values were then converted to percentages.

The value of a particular estuarine habitat for subyearling chinook salmon feeding was measured by an Index of Feeding:

$$IF = \frac{Ws}{Wf} \times 100\%,$$

where

IF = Index of Feeding,
Ws = weight of the stomach contents of a fish, and
Wf = weight of a fish.

The Mann-Whitney U statistic (Elliott 1977) was used to determine if there were significant differences in IF values between various habitats.

Results

Spatial and Temporal Distributions

Subyearling chinook salmon were collected throughout the estuary, but their distribution was not uniform. More than 95 percent of the subyearling chinook salmon were captured in intertidal (beach seines) and pelagic areas (purse seines). Catches in channel bottoms, tributaries, sloughs, and coves were small and were not further analyzed. Subyearling chinook salmon were captured in every month; however, they were most abundant from May through September (Figure 2).

Pelagic catches were lower in 1981 (prior to August) than in 1980; whereas those in intertidal areas were higher in 1981 than in 1980 (Figure 2). In 1980, peak abundance was bimodal (May and July) in pelagic areas of the upper estuary, but peak catches occurred in June in the lower pelagic habitat. In 1981, highest catches in pelagic areas occurred in July in both zones of the estuary. During June 1980 and 1981, peak catches occurred in intertidal areas of both the upper and lower estuary.

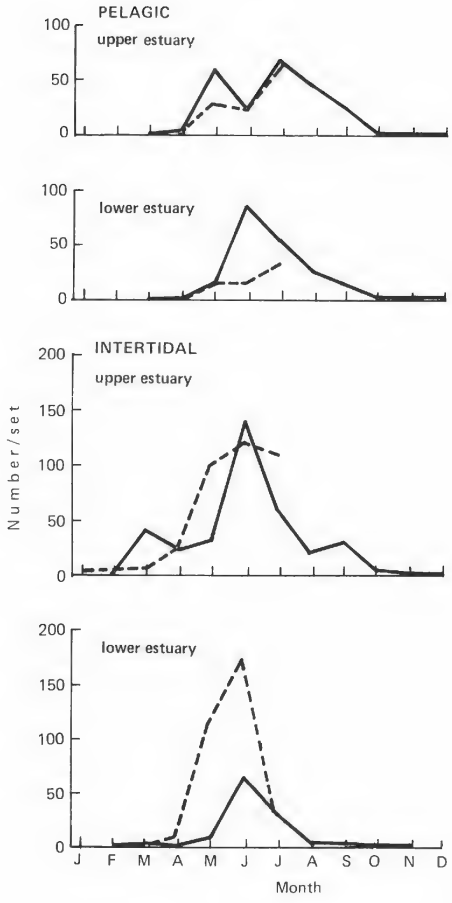

Figure 2. Catch per unit of effort of subyearling chinook salmon in four habitats of the Columbia River estuary. The solid line represents 1980 data and the dashed line represents 1981 data. Comparisons should not be made between pelagic and intertidal areas because of the use of different gear types.

Length Characteristics

During June, July, and September 1980, and in June and July 1981, subyearlings captured in pelagic areas of the lower estuary were significantly longer ($P \leq 0.05$) than subyearlings captured in pelagic areas of the upper estuary (Table 1). Comparisons were not made when $n \leq 20$ fish in a particular habitat. In intertidal areas of the lower estuary, juvenile chinook salmon were significantly longer than subyearlings in the intertidal upper estuary during May and July 1980, and May through July 1981.

From March to October the mean lengths of subyearling chinook salmon increased (Table 1). Mean lengths remained the same or declined in June. From May through August subyearlings collected in pelagic areas were significantly

TABLE 1. Lengths ($\bar{x}$ and 2SE; in mm) of subyearling chinook salmon collected in four habitats of the Columbia River estuary during 1980 and 1981.

Year and month	Pelagic						Intertidal					
	Upper estuary			Lower estuary			Upper estuary			Lower estuary		
	No.	$\bar{x}$	2 S E	No.	$\bar{x}$	2 S E	No.	$\bar{x}$	2 S E	No.	$\bar{x}$	2 S E
1980												
Feb	0	---	---	0	---	---	16	40.4	1.4	3	37.3	1.4
Mar	3	73.3	4.0	7	72.7	1.6	154	64.9	1.8	18	67.2	2.8
Apr	31	79.4	2.0	4	76.0	4.2	128	71.6	2.4	4	68.8	6.8
May	422	92.6	0.8	138	93.6	1.4	158	78.4	2.2	58	85.1	2.4
Jun	205	87.3	1.8	304	94.3	1.0	235	68.7	1.4	283	68.6	1.0
Jul	303	91.3	1.4	384	94.8	1.4	186	74.2	1.2	190	77.4	2.0
Aug	316	119.1	1.8	215	115.3	2.4	111	88.8	1.8	28	86.6	3.8
Sep	177	107.2	1.4	116	113.0	2.4	145	113.0	2.6	25	106.8	5.4
Oct	17	130.1	12.0	29	113.1	6.6	20	102.9	5.2	10	99.8	7.0
Nov	9	184.7	14.2	12	129.9	11.8	3	112.3	20.4	1	113.0	0.0
Dec	24	170.4	11.2	13	180.5	19.6	6	132.5	19.4	0	---	---
1981												
Jan	0	---	---	0	---	---	18	41.2	1.6	0	---	---
Feb	0	---	---	0	---	---	10	43.9	5.4	2	42.5	11.0
Mar	0	---	---	0	---	---	17	50.9	6.4	7	51.1	4.8
Apr	7	78.9	8.6	3	79.7	6.0	132	73.8	1.8	51	75.5	1.6
May	235	90.0	0.8	119	90.9	1.4	221	82.6	1.2	239	85.8	0.8
Jun	175	84.5	1.4	137	89.4	1.8	249	72.2	1.2	319	74.6	1.0
Jul	284	94.8	1.4	214	100.6	2.4	220	80.6	1.4	190	82.4	1.2

longer than those collected in intertidal habitats. In pelagic catches, there was an absence or paucity of subyearlings < 69 mm. In addition, subyearlings > 99 mm were not abundant in intertidal catches from May through August; yet they were common in pelagic catches.

Food Habits

A variety of food was consumed by juvenile chinook salmon (Table 2). Few subyearling chinook salmon were captured from October to February, so diet information from these months is not provided. Stomach analyses for 1981 were not completed due to financial constraints. The benthic amphipod *Corophium salmonis* was an important prey from March through July; however, in July, *C. salmonis* was only important in the intertidal habitat of the upper estuary. *Daphnia* spp. were important prey from July through September in pelagic habitats. In the intertidal habitat of the lower estuary, adult dipterans were important prey during April, May, August and September. Fish were important prey only in lower estuarine habitats (April and June).

Of the 762 stomachs examined from subyearlings collected from March through September, 12.3 percent were empty. The highest percentage of empty stomachs was found in the lower pelagic area (29.0 percent); the pelagic and intertidal habitats of the upper estuary had fewer empty stomachs ($\leq$ 6.7 percent).

Index of Feeding (IF) values for subyearlings collected in intertidal areas were significantly greater ($P \leq 0.05$) than those for subyearlings captured in pelagic habitats during all months except April (Table 3). Comparisons also were made between IF values for subyearling chinook salmon in intertidal habitats of the upper and lower estuary and in upper and lower pelagic habitats. The only significant differences were in June and September, when IF values were significantly higher in the upper pelagic habitats than in the lower pelagic habitats.

Effects of the Eruption of Mount St. Helens

Mount St. Helens erupted on 18 May 1980, resulting in the deposition of tremendous amounts of ash and mud in the Columbia River estuary. Turbidities in the estuary [River Kilometer (Rkm) 21] increased dramatically—1120 Nephelometric

TABLE 2. Food of subyearling chinook salmon captured in four Columbia River estuary habitats from March through September 1980. The importance of a particular food is estimated as percent Index of Relative Importance (n = sample size; values < 1.0 are not shown).

Prey items	MARCH 1980				APRIL 1980				MAY 1980				JUNE 1980			
	Lower pelagic n=3 0 empty	Upper pelagic n=3 0 empty	Lower intertidal n=11 0 empty	Upper intertidal n=20 3 empty	Lower pelagic n=4 1 empty	Upper pelagic n=20 1 empty	Lower intertidal n=4 1 empty	Upper intertidal n=19 0 empty	Lower pelagic n=30 5 empty	Upper pelagic n=33 0 empty	Lower intertidal n=20 1 empty	Upper intertidal n=21 0 empty	Lower pelagic n=45 20 empty	Upper pelagic n=45 2 empty	Lower intertidal n=30 2 empty	Upper intertidal n=25 0 empty
Mysidacea	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Neomysis mercedis	—	3.4	14.2	9.1	—	—	9.6	—	—	—	2.7	4.9	—	—	2.5	6.4
Cumacea	—	—	—	—	—	—	1.5	—	—	—	—	—	—	—	1.1	—
Amphipoda	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Eogammarus spp.	—	—	8.0	—	—	—	—	—	—	—	—	—	7.9	—	3.2	3.3
Eogammarus oclari	—	—	—	—	—	—	—	—	—	—	—	—	—	—	3.4	—
Ampithoe spp.	—	—	—	—	—	—	—	—	—	—	—	—	2.6	—	—	—
Corophium spp.	27.6	—	—	—	—	—	—	—	—	—	—	—	5.3	—	—	—
Corophium salmonis	—	4.5	73.7	88.8	37.2	84.0	11.5	52.4	81.7	74.9	9.5	90.4	5.7	4.6	48.8	68.5
Corophium spinicorne	—	—	—	—	—	10.1	—	3.1	1.1	10.7	—	—	7.7	—	—	—
Eohaustorius estuaris	—	—	—	—	—	—	—	—	—	—	3.1	—	—	—	—	—
Decapoda	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Crangon franciscorum	—	—	—	—	—	—	—	—	—	—	—	—	—	—	2.5	—
Cancer magister (megalops)	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Cladocera	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Daphnia spp.	60.6	—	1.2	—	—	—	—	—	—	3.4	—	1.1	1.2	4.2	2.1	2.2
Copepoda	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Calanoida	—	—	—	—	—	—	—	—	—	—	—	—	1.4	—	20.5	—
Cyclopoida	—	—	—	—	—	—	—	—	—	—	—	—	2.4	—	—	—
Harpacticoida	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1.2	—
Insecta	—	—	—	—	—	—	16.0	—	—	—	—	—	—	—	—	—
Diptera (adult)	—	5.1	1.8	—	—	—	72.8	4.7	1.9	7.7	71.0	3.1	15.2	81.2	3.6	6.2
Heleidae (larvae)	—	—	—	—	—	—	—	—	—	—	—	—	3.0	—	—	4.6
Chironomidae (larvae)	—	—	—	—	—	1.4	1.4	—	—	—	—	—	—	1.2	—	7.5
Chironomidae (pupae)	—	55.0	—	—	—	2.1	—	13.5	—	—	—	—	—	—	—	—
Isoptera	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Coleoptera	—	1.7	—	—	—	—	—	1.6	—	—	—	—	—	1.1	—	—

TABLE 2. Continued

Prey items	MARCH 1980				APRIL 1980				MAY 1980				JUNE 1980			
	Lower pelagic n=3 0 empty	Upper pelagic n=3 0 empty	Lower intertidal n=11 0 empty	Upper intertidal n=20 3 empty	Lower pelagic n=4 1 empty	Upper pelagic n=20 1 empty	Lower intertidal n=4 1 empty	Upper intertidal n=19 0 empty	Lower pelagic n=30 5 empty	Upper pelagic n=33 0 empty	Lower intertidal n=20 1 empty	Upper intertidal n=21 0 empty	Lower pelagic n=45 20 empty	Upper pelagic n=45 2 empty	Lower intertidal n=30 2 empty	Upper intertidal n=25 0 empty
Hymenoptera	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Plecoptera	—	—	—	1.0	—	—	—	—	—	—	—	—	—	—	—	—
Hemiptera	—	—	—	—	—	—	2.4	—	—	—	—	—	—	—	—	—
Homoptera	—	—	—	—	—	—	—	—	11.3	—	—	—	4.0	1.5	—	—
Collembola	—	6.4	—	—	—	—	—	18.6	—	—	—	—	2.2	—	—	—
Insect parts	11.8	19.0	—	—	—	—	—	4.4	—	1.3	—	—	—	—	—	—
Arachnida	—	1.7	—	—	—	—	—	—	—	—	—	—	—	3.2	—	—
Teleostei	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Engraulis mordax	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Allosmerus elongatus	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Spirinchus thaleichthys	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Ammodytes hexapterus	—	—	—	—	—	—	—	—	—	—	2.0	—	—	—	7.5	—
Digested fish	—	—	—	—	19.1	—	—	—	3.6	—	9.2	—	22.4	—	—	—
Larval fish	—	—	—	—	43.7	—	—	—	—	—	—	—	—	—	—	—
Plant material	—	3.2	—	—	—	—	—	—	—	—	—	—	16.4	—	—	—

TABLE 2. (Continued)

Prey items	JULY 1980				AUGUST 1980				SEPTEMBER 1980			
	Lower pelagic n=47 9 empty	Upper pelagic n=57 6 empty	Lower intertidal n=33 1 empty	Upper intertidal n=22 1 empty	Lower pelagic n=60 22 empty	Upper pelagic n=58 8 empty	Lower intertidal n=20 3 empty	Upper intertidal n=22 0 empty	Lower pelagic n=32 7 empty	Upper pelagic n=36 0 empty	Lower intertidal n=18 1 empty	Upper intertidal n=24 0 empty
Mysidacea	—	—	—	—	—	—	—	—	—	—	—	—
Neomysis mercedis	—	—	—	—	—	—	—	19.6	—	—	—	1.0
Cumacea	—	—	—	—	—	—	—	—	—	—	—	—
Amphipoda	—	—	—	—	—	—	—	—	—	—	—	—
Eogammarus spp.	—	—	2.5	—	—	—	—	—	—	—	—	—
Eogammarus oclari	—	—	—	—	—	—	—	—	—	—	—	—
Ampithoe spp.	—	—	—	—	—	—	—	—	—	—	—	—
Corophium spp.	—	—	—	—	—	3.3	—	—	—	—	—	—
Corophium salmonis	—	—	13.2	78.1	—	—	—	—	—	—	—	3.2
Corophium spinicorne	—	1.0	2.4	—	—	—	—	—	—	—	—	—
Eohaustorius estuaris	—	—	—	—	—	—	2.7	—	—	—	—	—
Decapoda	—	—	—	—	—	—	—	—	—	—	—	—
Crangon franciscorum	—	—	—	—	—	—	—	—	—	—	—	—
Cancer magister (megalops)	—	—	—	—	2.6	—	—	—	—	—	—	—
Cladocera	—	—	—	—	—	—	—	—	—	—	—	—
Daphnia spp.	90.4	43.0	5.1	8.9	74.1	95.4	7.9	79.1	72.6	99.7	—	6.0
Copepoda	—	—	—	—	—	—	—	—	—	—	—	—
Calanoida	—	2.2	24.3	1.2	—	—	1.0	—	—	—	—	—
Cyclopoida	1.6	3.0	—	—	—	—	3.3	—	—	—	—	—
Harpacticoida	—	—	—	—	—	—	—	—	—	—	—	—
Insecta	—	—	—	—	—	—		—	—	—	—	—
Diptera (adult)	1.2	7.5	11.3	4.3	—	—	26.6	—	1.7	—	21.8	13.5
Heleidae (larvae)	—	15.5	—	—	—	—	—	—	—	—	—	—
Chironomidae (larvae)	—	5.2	—	—	—	—	—	—	—	—	—	—
Chironomidae (pupae)	—	—	—	—	—	—	—	—	—	—	—	—
Isoptera	—	—	—	—	—	—	—	—	—	—	—	3.6
Coleoptera	—	16.7	—	—	—	—	—	—	—	—	—	—

TABLE 2. Continued

Prey items	JULY 1980				AUGUST 1980				SEPTEMBER 1980			
	Lower pelagic n=47 9 empty	Upper pelagic n=57 6 empty	Lower intertidal n=33 1 empty	Upper intertidal n=22 1 empty	Lower pelagic n=60 22 empty	Upper pelagic n=58 8 empty	Lower intertidal n=20 3 empty	Upper intertidal n=22 0 empty	Lower pelagic n=32 7 empty	Upper pelagic n=36 0 empty	Lower intertidal n=18 1 empty	Upper intertidal n=24 0 empty
Hymenoptera	—	3.3	14.9	—	—	—	27.9	—	—	—	2.6	22.6
Plecoptera	—	—	—	—	—	—	—	—	—	—	—	—
Hemiptera	—	—	—	—	15.3	—	1.2	—	—	—	—	—
Homoptera	—	—	—	—	—	—	10.0	—	11.9	—	33.2	4.1
Collembola	—	—	—	—	—	—	—	—	—	—	—	—
Insect parts	—	—	2.6	3.0	—	—	17.0	—	1.1	—	37.2	45.1
Arachnida	—	—	—	1.7	—	—	—	—	—	—	—	—
Teleostei	—	—	—	—	—	—	—	—	—	—	—	—
Engraulis mordax	—	—	18.9	—	—	—	—	—	—	—	3.3	—
Allosmerus elongatus	2.4	—	—	—	—	—	—	—	—	—	—	—
Spirinchus thaleichthys	2.7	—	—	—	3.5	—	—	—	—	—	—	—
Ammodytes hexapterus	—	—	—	—	—	—	—	—	—	—	—	—
Digested fish	—	—	—	—	2.3	—	—	—	11.8	—	—	—
Larval fish	—	—	—	—	—	—	—	—	—	—	—	—
Plant material	—	—	—	—	—	—	—	—	—	—	—	—

TABLE 3. Comparisons of Index of Feeding (IF) values, using the Mann-Whitney U statistic, for subyearling chinook salmon *Oncorhynchus tshawytscha* captured in two habitats in the Columbia River estuary, 1980 (* $P < 0.05$, *** $P < 0.001$).

Month	Habitat	Sample size	IF median (%)	U
Mar	Pelagic	6	.050	64.5*
	Intertidal	31	.260	
Apr	Pelagic	24	.250	587.0
	Intertidal	23	.140	
May	Pelagic	63	.260	2842.5***
	Intertidal	41	.780	
Jun	Pelagic	90	.070	5961.5*
	Intertidal	55	.130	
Jul	Pelagic	104	.030	6864.0***
	Intertidal	55	.180	
Aug	Pelagic	118	.020	7871.5***
	Intertidal	42	.300	
Sep	Pelagic	68	.135	3220.0***
	Intertidal	42	.440	

Turbidity Units (NTU) on the surface 3 days after the eruption. Normal turbidity is <10 NTU. Subyearling chinook salmon catches in pelagic areas of the upper estuary decreased substantially in June. This large decline was not repeated in 1981, suggesting that the eruption may have been responsible for the 1980 change; however, other factors such as timing of large hatchery releases may have influenced catches. The eruption probably had little effect on the 1980 feeding habits of subyearling chinook salmon, except in June. May sampling in pelagic and intertidal habitats was completed prior to the eruption of the volcano.

Discussion

Distribution

Because we sampled monthly at each station, our catches indicate only general trends in relative abundance of subyearling chinook salmon in the Columbia River estuary. Large groups of hatchery fish migrate through the estuary during the spring and summer. Sampling only monthly at each station increases the probability of not collecting large numbers of subyearling chinook salmon from particular hatchery releases. Intensive sampling at a particular site(s) is necessary to define migrational peaks and timing (Dawley *et al.* 1981, 1982).

The relative abundance of subyearling chinook salmon in areas (i.e., tributaries, sloughs, and coves) sampled with trapnets may have been underestimated. Some subyearling chinook salmon may have swum over or under the narrow stationary leads of the trapnets. In addition, some subyearling chinook salmon may have swum through the leads of the trapnets, particularly those that contained 44.4 mm mesh netting.

Residence Time

Other researchers observed that juvenile subyearling chinook salmon have extended residences in estuaries. In the Sixes River estuary in southern Oregon, Reimers (1973) found that subyearling fall chinook salmon remained in the estuary for up to about three months. Healey (1980) estimated an average residency of 25 days for individual fish in the Nanaimo River estuary, British Columbia.

It is difficult to ascertain how long individual subyearling chinook salmon remain in the Columbia River estuary because of the various groups of wild and hatchery fish that enter the estuary in the spring and summer. Releases of hatchery subyearling chinook salmon into the Columbia River system exceeded 91 million fish in both 1980 and 1981. Juveniles enter the

estuary primarily from the Columbia River, but significant numbers also enter through tributaries of the estuary.

Length Characteristics

Many subyearling chinook salmon enter the Columbia River estuary at a larger size than those entering other estuaries, such as the Nanaimo River estuary in British Columbia (Healey 1980) and the Sacramento-San Joaquin estuary in California (Kjelson *et al.* 1982). The mean length of subyearlings in the Columbia River estuary increased from March to October; however, size variation cannot be attributed solely to growth in the estuary. Subyearlings continually enter the estuary throughout the year. Hatchery releases of different sized fish were responsible for some of these length changes. The decline, or at least lack of increase, in the mean length of subyearlings in June was probably due to a large hatchery release(s) of smaller juvenile chinook salmon.

Dawley *et al.* (1979) observed that subyearling chinook salmon collected in beach seines at Rkm 6-8 (April-August) were only slightly larger than those collected at Rkm 75. We observed a similar size pattern between the upper and lower estuary intertidal sites from May through July.

Length differences between subyearlings collected in intertidal and pelagic habitats (Table 1) indicated that larger subyearlings preferred pelagic areas. The scarcity of subyearlings < 69 mm in pelagic catches could have been caused by gear selectivity and/or by avoidance of pelagic areas by smaller fish. Although mesh sizes in the purse seines and beach seines were similar, the purse seine contained a larger percentage of mesh through which smaller subyearlings could escape. However, gear selectivity did not account for the reduced beach seine catches of subyearlings > 99 mm during the late spring and summer, since they were captured in purse seines. A logical explanation is that, in general, larger subyearlings prefer open water to the shallow intertidal habitats of the estuary. Myers (1980) observed that the mean length of juvenile chinook salmon collected in channel areas was greater than that of those collected in intertidal areas. Dawley *et al.* (1982) observed similar size distributions at Jones Beach (Rkm 75), Columbia River.

Food Habits

The food habits of subyearling chinook salmon in other Pacific Northwest estuaries have been studied by Sasaki (1966), Herrmann (1971), Levy and Levings (1978), Levy *et al.* (1979), Healey (1980), Myers (1980), Meyer *et al.* (1981), and Pearce *et al.* (1982). The amphipod *Corophium salmonis* was an important prey in the lower San Joaquin River, California (Sasaki 1966); Grays Harbor, Washington (Herrmann 1971); Duwamish estuary, Washington (Meyer *et al.* 1981); and the Columbia River estuary (this study).

The Columbia River estuary is an important foraging area for subyearling chinook salmon. Although subyearlings feed in pelagic areas, intertidal areas are used more intensively. The higher IF values for subyearling chinook salmon in intertidal habitats are probably related to prey distributions and abundances. Large populations of *Corophium salmonis* occur in many intertidal areas of the Columbia River estuary (Durkin and Emmett 1980). Commonly eaten insect species, such as chironomids, may also be found in the tidal flats and/or marsh areas. The IF differences between intertidal and pelagic subyearling chinook salmon in July through September were apparently related to the importance of *Daphnia* spp. as a prey item in pelagic habitats. *Daphnia* spp. are relatively small zooplankters; consequently, many have to be consumed to equal the biomass of one larger invertebrate.

Differences in IF values for subyearling chinook salmon feeding in intertidal and pelagic habitats could also be caused by fish behavior. Subyearling chinook salmon in pelagic habitats may be actively migrating to the ocean, spending little time pursuing prey. This could explain the high percentage of empty stomachs found in the lower pelagic habitat. Subyearling chinook salmon in the intertidal zones are generally shorter in mean length than those in the pelagic zones, and may not be migrating as rapidly and spending more time searching for food.

Why subyearling chinook salmon switched from feeding primarily on *C. salmonis* during the spring and early summer to other prey in later months is unclear. Possibilities include changes in *C. salmonis* behavior and/or abundance, or increases in the relative abundances of other prey. For example, *Daphnia* spp. populations peak in

July-August (Haertel and Osterberg 1967). The dietary importance of *C. salmonis* coincided with the spring freshet. Information regarding the effects of the spring freshet on *C. salmonis* populations is lacking and needs to be studied.

The Columbia River estuary is important in the life history of subyearling chinook salmon. Intertidal areas are especially important feeding habitats. Unfortunately, it is these intertidal areas that have the greatest potential for alteration or are already threatened by development. These areas must be preserved to maintain suitable habitat for subyearling chinook salmon in the Columbia River estuary.

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Influence of Substratum on the Comparative Food Habits of Two Species of Estuarine Stichaeoid Fishes, *Anoplarchus purpurescens* (Family Stichaeidae) and *Pholis ornata* (Family Pholididae)

Abstract

Food habits of two species of co-existing northeast Pacific estuarine stichaeoid fishes, *Anoplarchus purpurescens* and *Pholis ornata,* were studied by analysis of gut contents of specimens collected over two types of substrata, muddy and rocky. *A. purpurescens* fed on a greater range of invertebrates and also consumed a substantial quantity of algae with macrophytes reported in over 76 percent of individuals of this species. *P. ornata* fed upon fewer kinds of prey items, consuming chiefly amphipods over rock substrata and siphon tips of bivalves over muddy substrata. Cropping of exposed parts of macroinvertebrates appears to be an important feeding strategy for both species. Differences in diet between the two species and the capacity to shift food preferences based on substrate-related prey availability may serve to accommodate the coexistence of these two morphologically and ecologically similar species.

Introduction

Intertidal fishes of North Pacific shores may exhibit specific substratum preferences and the range of microhabitats and associated feeding opportunities that are available may be significant in structuring the intertidal ichthyofaunal community. In his comprehensive reviews of intertidal fish biology, Gibson (1969, 1982) concluded that rocky shores with highly irregular topography provide the greatest amount of cover and hence display the greatest diversity of species. Studies by Nakamura (1976) have revealed differing substratum preferences in sympatric species of sculpins of the family Cottidae. Marliave (1977) demonstrated that settling larvae of several species of North Pacific intertidal fishes exhibit specific substratum preferences usually selecting substrata that are representative of adult microhabitats.

Stichaeoid fishes of the families Stichaeidae and Pholididae are especially intriguing owing to their amphibious nature. Stichaeoids have been shown to occur in greater frequency over substrata that are periodically exposed during low tide (Yoshiyama 1981). Two species of amphibious stichaeoids, *Anoplarchus purpurescens* and *Pholis ornata,* broadly overlap in distribution and microhabitat preferences in Yaquina Bay, a small Oregon estuary with both muddy and rock susbstrata (Barton 1982a). *A. purpurescens* has been found in rocky and muddy substrata in both open coastal waters and sheltered embayments (Schultz and Delacy 1932; Yoshiyama 1981; Barton 1982a,b). Fishes of the family Pholididae are associated with rocky microhabitats (Quasim 1957, Sawyer 1967) but also demonstrate a pronounced affinity for vegetation (Burgess 1978). *P. ornata* constitutes a significant component of the intertidal ichthyofauna associated with eelgrass in Yaquina Bay (Bayer 1981).

The question of competitive interaction based on available food resources is a difficult one to assess. In North Pacific intertidal ichthyofaunal communities, possible competition for food, measured as dietary overlap, has been implicated in tidepool cottids (Yoshiyama 1980). An absence of resource partitioning among cottids may also reflect an ample abundance of food in the intertidal zone such that competitive interactions do not exist in sympatric species (Nakamura 1971). Studies of the comparative food habits of several species of stichaeoids suggest mechanisms of resource allocation among sympatric species (Barton 1982b). Differential allocation of food resources may facilitate the observed overlap in substratum and microhabitat preferences exhibited by *A. purpurescens* and *P. ornata* in Yaquina Bay. Although these two species are frequently found co-existing beneath the same rock or clump of vegetation at low tide, they may possess decidedly different food preferences and foraging strategies which may vary over different substrata at high tide. The purpose of this study was to compare the food habits of these two species so that an evaluation of the influence

of inhabited substratum and its impact on competitive interactions might be possible.

Materials and Methods

Fishes were collected for analysis of stomach contents from three sites within Yaquina Bay (44°37'N; 124°02'W), a small tidal estuary on the central Oregon coast. The estuary consists of a narrow channel bordered with mudflats and cobble beaches. Fishes were collected at each of three stations within the Bay (Figure 1) and the nature of the substratum (rocky or muddy) recorded for each collection. While both bottom types could be observed at each station, stations 1 and 3 consisted predominantly of a hard mudstone substratum with patches of loose cobble while station 2 was chiefly broad mudflats with a seasonal cover of eelgrass (*Zostera*) or sea lettuce (*Ulva*) and patches of loose cobble scattered throughout.

All fishes were collected during mid-morning low tides in the spring and summer 1976-1977. Fishes were captured beneath loose boulders and in vegetation with the aid of aquarium dipnets and were immediately preserved in a buffered solution of 10 percent formalin in seawater. Preservation of gut contents was facilitated in larger (>60 mm) individuals by injection of the formalin solution into the gut cavity. Digestive tracts were later removed and contents identified to the lowest possible taxon. Foor overlap was measured as the percentage of similarity (PS) (Whittaker 1967, McEachran *et al.* 1976). This value was calculated from the number of individual food items constituting the diet of each

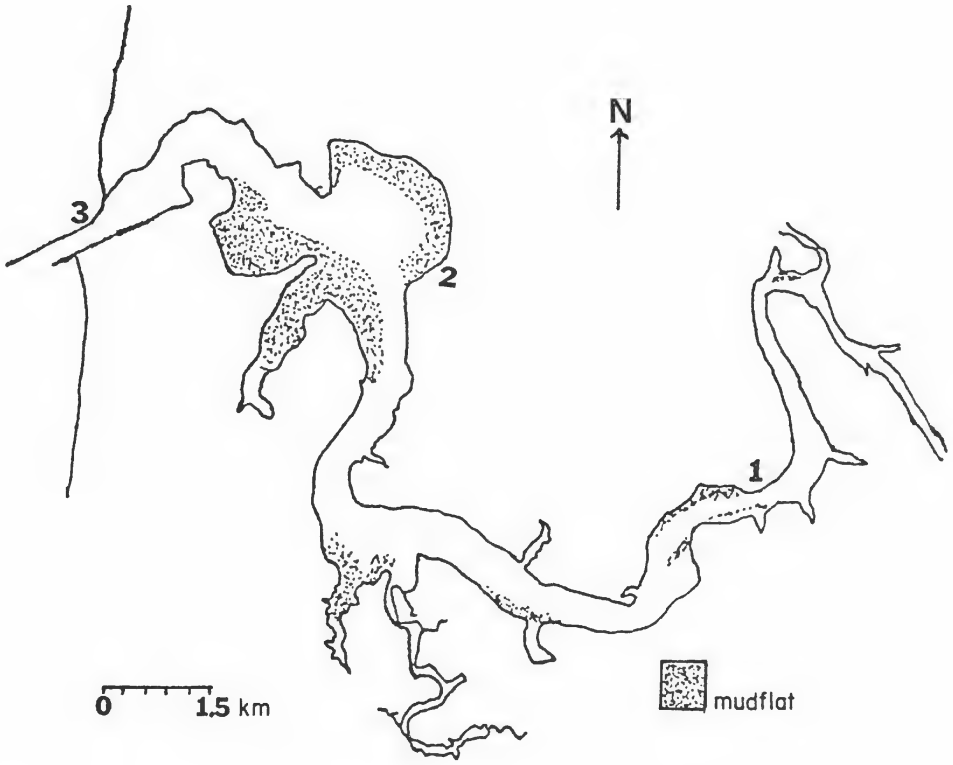

Figure 1. Map of Yaquina Bay, Oregon, showing collection sites.

species and each substratum type. Values less than 50 percent were judged to be significant (McEachern *et al.* 1976).

Results

A total of 511 stomachs, representing both species over both types of substrata, was examined. Of the two species, *A. purpurescens* appears to select from a broader range of food items (Table 1, Figure 2). Among the most noteworthy differences in the diets of the two species is the substantial quantity of macroalgae found in the stomachs of *A. purpurescens.* Nemerteans and polychaetes also appear in greater numbers in this species, especially over rocky substrata (Table 2, Figure 2). *P. ornata* exhibited a greater specificity in diet and substratum appears to have an impact upon food preferences in this species. Amphipods constitute the chief food source for *P. ornata* over rocky surfaces but this species shifts to a bivalve siphon nipping strategy when foraging over muddy surfaces (Figure 2). Cropping of exposed parts of benthic infauna appears to be an important strategy employed by both species. Barnacle cirri, heads and tentacle crowns of polychaetes, and the aforementioned siphons were observed in the stomachs of both *A. purpurescens* and *P. ornata.* Only an incidental consumption of algae was observed in *P. ornata,* however.

Calculations of PS values were based on the five most frequently recovered animal food items which constituted the bulk of the stomach content (Table 2). The PS value for *A. purpurescens* in rocky vs. muddy substratum was 61.8 percent; for *P. ornata* in rocky vs. muddy substratum, 41.5 percent. Overall PS value for *A. purpurescens* vs. *P. ornata* was 75.1 percent. Although constituting a substantial quantity of the stomach volume in *A. purpurescens,* algae was not included because of the impossibility of enumerating individual organisms. Both species emphasize the consumption of small crustacea, mainly amphipods. The

TABLE 1. Food preferences of *Anoplarchus purpurescens* and *Pholis ornata* measured as total number and percent occurrence of individuals from different substrata with specified food items in stomach contents.

	Anoplarchus purpurescens				Pholis ornata			
	total number		percent occurrence		total number		percent occurrence	
Food Item	*rocky*	*muddy*	*rocky*	*muddy*	*rocky*	*muddy*	*rocky*	*muddy*
Algae	84	88	76.4	76.5	7	13	7.4	8.8
Nematoda	5	3	4.5	2.6	0	1	0	.7
Nemertinea	40	3	36.4	2.6	1	4	1.1	2.7
Polychaeta	40	23	36.4	20.0	4	13	4.3	8.8
Bivalva (siphons)	13	21	11.8	17.4	1	109	1.1	74.2
Gastropoda	0	1	0	.9	0	0	0	0
Amphineura	1	0	.9	0	0	0	0	0
Cirripedia	1	5	.9	4.3	12	1	12.8	.7
Copepoda	9	2	8.2	1.7	1	17	1.1	11.6
Ostracoda	0	0	0	0	2	0	1.4	0
Cumacea	1	4	.9	3.5	5	0	5.3	0
Amphipoda	38	82	34.5	71.3	73	34	77.7	23.1
Isopoda	6	17	5.5	14.8	15	2	16.0	1.4
Decapoda	9	13	8.1	11.3	8	41	8.5	27.9
Pycnogonida	7	4	6.4	3.5	0	0	0	0
Insecta	8	2	7.3	1.7	3	0	3.2	0
Number with empty stomachs	4	16	—	—	12	13	—	—
Total number of sample	114	131			106	160		

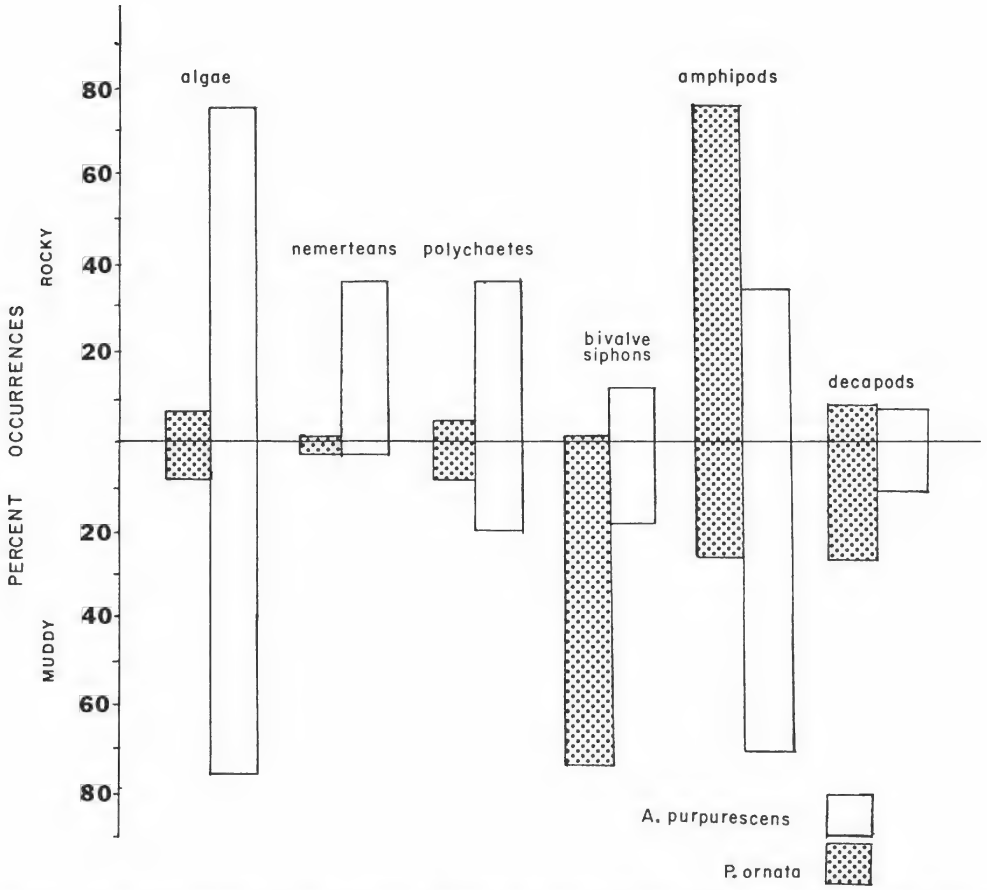

Figure 2. Percent occurrences of the most frequently observed food items in the guts of *A. purpurescens* and *P. ornata* feeding over rocky vs. muddy substrata.

significance of substratum type is apparent in *P. ornata* with a low PS value of 41.5 percent calculated from a comparison of the animal components of diets from individuals collected over rocky versus muddy surfaces.

Discussion

The extent to which coexisting species allocate resources or, in absence of such allocation, have resource-impacted ranges of distribution is difficult to assess. Gibson (1969, 1982) has summarized some of the strategies that alleviate competition for available food resources among sympatric intertidal fish species. Substratum related types of foraging patterns may facilitate coexistence in estuaries by emphasizing different components of overlapping diets. This may be interpreted as a response to changes in feeding opportunities in the intertidal zone of estuaries. The high dietary overlap reported for *A. purpurescens* and *P. ornata* in this study is largely a consequence of a heavy dependence upon small amphipods by both species. This value also does not reflect the significance of herbivory in the foraging strategy of *A. purpurescens.* An analysis of dietary overlap that relies upon enumeration of individual prey items in the gut contents is not without its limitations. Numerical methods may over-emphasize small prey items taken in large numbers (for example, amphipods) yet such

TABLE 2. Number of individual animal food items in stomachs of *A. purpurescens* and *P. ornata* inhabiting different substrata.

	A. purpurescens		*P. ornata*	
Food Item	*rocky*	*muddy*	*rocky*	*muddy*
Nematoda	5	5	0	0
Nemertinea	114	9	0	4
Polychaeta	70	22	10	18
Bivalva (siphons)	20	27	8	595
Gastropoda	0	1	0	0
Amphineura	2	0	0	0
Cirripedia	1	5	11	4
Copepoda	22	2	3	29
Ostracoda	0	0	0	2
Cumacea	1	6	4	0
Amphipoda	86	483	460	116
Isopoda	6	76	28	2
Decapoda	9	17	5	65
Pycnogonida	8	5	0	0
Insecta	19	3	4	0

methods may give a better indication of feeding effort (Hyslop 1980). Small organisms may also be of enhanced significance because of their greater speed of digestion (Sikora *et al.* 1972 in Hyslop 1980).

Soft bodied invertebrates appear in greater quantities in the diet of *A. purpurescens,* especially in rocky substrata. The cirratulid polychaete tentacles observed in the guts of *A. purpurescens* in this and other studies (Barton 1982b, Yoshiyama and Darling 1982) suggest an unusual dietary adaptation that may facilitate coexistence with sympatric species. Yoshiyama and Darling (1982) have demonstrated that cirratulid polychaetes are distasteful to other fish species.

The most noteworthy difference in the diets of *A. purpurescens* and *P. ornata* was in the consumption of large quantities of macroalgae by the former. Macrophytes can provide significant nutrition for fishes (Montgomery and Gerking 1980) and their utilization has been demonstrated to be an ecologically and energetically feasible strategy for north temperate fishes, including some species of stichaeoids (Wells *et al.* 1973; Edwards and Horn 1982; Horn, Murray, and Edwards 1982; Horn 1983). In related studies, Barton (1982b) demonstrated food resource partitioning in central California intertidal stichaeoid communities that included *A. purpurescens,* and Hughes (1983) has shown a reduction in the dietary overlap in two species of *Pholis,* including *P. ornata,* that coexist in a shallow inlet of Puget Sound.

Since both species are basically predators upon the epifaunal and infaunal components of benthic communities, substratum-related variation in foraging strategies might be expected. This was most apparent with *P. ornata* that switched from a chiefly amphipod diet in rocky areas to one consisting mainly of bivalve siphon tips in muddy areas. Hughes (1983) also reported siphon nipping in *P. ornata* in Puget Sound and suggested that this species possesses dentition that facilitates this mode of feeding. Peterson and Quammen (1982) have observed siphon nipping to be an important component in the diet of three inshore fish species and have demonstrated significant decreases in growth rates of bivalve populations exposed to siphon cropping by small fishes. The dependence upon siphons by *P. ornata* reflects its preference for muddy, protected embayments whereas the greatest diversity in stichaeoid communities is seen in rocky shores in more exposed locales (Hart 1973, Miller and Lea 1972, Yoshiyama 1981).

The relationship between substratum and feeding strategy has been documented in a number of benthic fish species including skates (McEachran *et al.* 1976) and flatfishes (Pearcy and Hancock 1978). The present study demonstrates that the coexistence of *Anoplarchus purpurescens* and *Pholis ornata* may be facilitated by differences in feeding preferences with *A. purpurescens* consuming a greater variety of food items, including substantial quantities of algae, while *P. ornata,* with a more restricted dietary regime, demonstrates a shift in dietary preferences based on the nature of the substratum over which it is feeding.

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An Aerial Census of Mountain Goats in the Olympic Mountain Range, Washington

Abstract

Mountain goats were introduced into the Olympic Mountains, Washington, during the late 1920s and are now considered an exotic species in Olympic National Park. We report the results from the first extensive aerial census of this introduced population. A series of population reductions in the Klahhane Ridge area of the park was used to estimate a census efficiency of 66 percent. The goat population in the 50,063 ha census zone was estimated at 1175 ± 171(SE) during July 1983.

Introduction

Mountain goats (*Oreamnos americanus*) were introduced into the Olympic Mountains from 1925-29 and have since dispersed throughout the range (Moorhead and Stevens 1977; Stevens 1979, 1983). Olympic National Park was established in 1938 to be managed as a natural area with the primary purpose of preserving representative natural ecosystems. Goats are now seen as an exotic species with the capacity to alter pristine ecological relationships (National Park Service 1981).

The National Park Service initiated a three-year experimental goat management program in Olympic National Park during 1981. One aspect of the program involved removing goats from an area to measure the population's response to control (Aho *et al.* 1982, 1984). This experimental approach to management, where small scale management operations are used to test research hypotheses and to guide operational management (Macnab 1983), seems to have the potential to provide additional useful information on goat ecology. Development of reliable population inventory techniques for mountain goats has been identified recently as the most important research priority (Eastman 1977). We report here the results from the first extensive aerial census of mountain goats in the Olympic Range, where population reductions are used to estimate census efficiency.

Stevens (1980) estimated that goat population in the Olympic Mountains at about 550-880 animals in 1980; about 85-90 percent were thought to occur within the park. These estimates were based upon ground censuses of 10 subpopulations, field surveys of goat distribution, and educated guesses for other areas based upon reports of hikers and hunters. Since park managers were considering an extensive goat removal program as one management option, a more comprehensive population estimate was needed.

Study Area and Methods

Previous studies have shown that the mountain goat population is distributed discontinuously as "nodes" or subpopulations throughout the Olympics. They are seasonally migratory, with summer ranges mostly above 1,500 m. Summer and winter ranges overlap for some subpopulations, although seasonal ranges may be separated by as much as 8 km in other areas. Goats may occupy winter ranges above 1,500 m, although others winter on rock outcrops as low as 300 m (Stevens 1979, 1980, 1983).

The census zone included all of the 50,063 ha of land free of glacial ice above 1,520 m (5,000 feet) in the Olympics (Figure 1). About 85 percent of the zone is within Olympic National Park. A block count sampling method was chosen because of the extremely precipitous terrain and the highly variable goat densities. We drew heavily upon past studies (Stevens 1979, 1980, 1983) and the extensive knowledge of V. Stevens and her co-workers to delineate four census strata:

(1) Known high density goat areas: Royal Basin, Appleton Pass, Lake Constance-Charlia Lakes. 5,071 ha (Figure 1). Aerial total counts were attempted in each unit.
(2) Known or suspected low density goat areas: 13,135 ha. (Densities guessed to be 0.20 goats/km^2 or less). These were divided into 26 blocks of about 500 ha each. Six blocks (23 percent) were chosen randomly and censused.

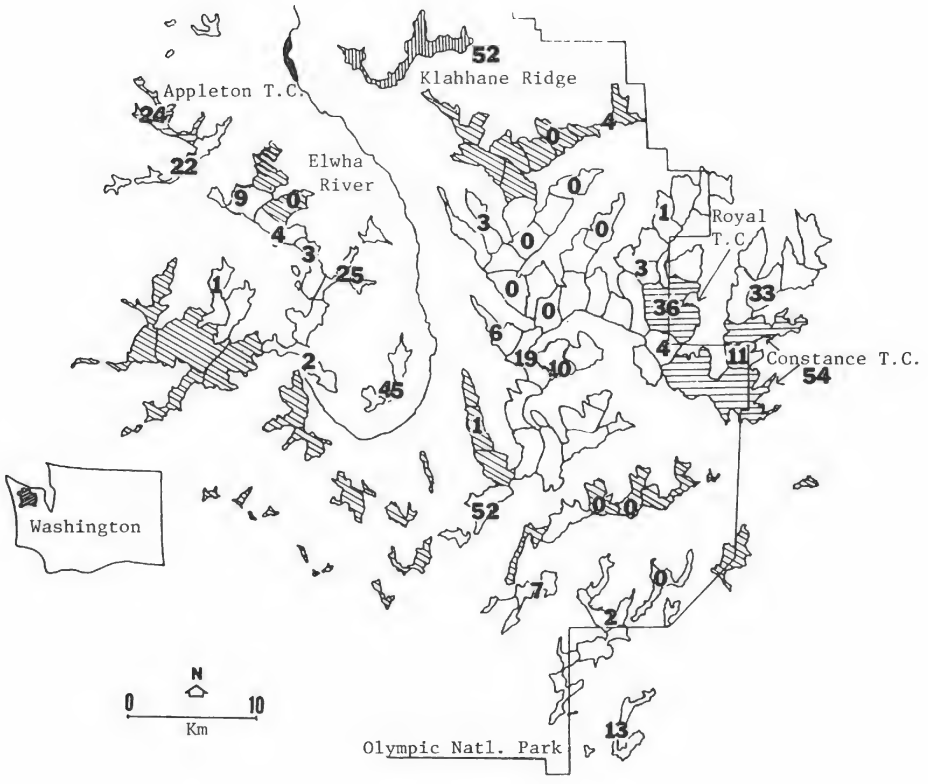

Figure 1. Mountain goat census units and numbers counted by unit, Olympic Mountains, July 1983. Total count (TC), Klahhane Ridge, low density (diagonal cross hatch), and medium density units are indicated. Extensive areas of glacial ice in some units are not shown.

(3) Known or suspected medium density goat areas: 29,860 ha. These were divided into 59 blocks of about 500 ha each. Twenty-eight (47 percent) were chosen randomly and censused.

(4) Klahhane Ridge: 1,997 ha. Censused separately using the "Index-Manipulation-Index" technique (see below).

The census design requires explanation. Late July was chosen to conduct the census because most goats occupy open summer ranges above timberline and they are conspicuous against the low, green vegetation. Also, increased temperatures during August often drive goats back down into forests. The 500 ha blocks represented a compromise between goat home range size (Stevens 1980), the amount of area to be sampled, and the observation that lower sampling errors usually occur when many small units are counted rather than a few large ones (Norton-Griffiths 1978). Information on goat densities, though extensive, was still limited for certain areas. Thus, sampling intensity also represented a series of compromises. Six blocks sampled in the putative low density stratum represented a guess at the minimum required to calculate an acceptable estimate. Great variation was expected among the supposed medium density blocks (representing all areas between the high density stratum of perhaps 3-6 goats/km^2

and the low density stratum of 0.2/km²); 28 blocks were chosen as the maximum that was economically feasible to count.

Census blocks were delineated on 1:62,500 scale contour maps with an Apple II graphics digitizer. Blocks were designed to include as many slopes and aspects as possible. This design was chosen because goats move frequently about the different slope exposures in response to short-term changes in temperature, snow melt, and vegetation growth.

Conspicuous terrain features (glaciers, rock outcrops, trails, forest strips) were used as block boundaries. Lower boundaries of each block were checked in the field against the aircraft altimeter. Occasionally, a block was produced by combining the areas of several disjunct peaks or ridges (Figure 1). Block size averaged 506 ± 52 ha. A maximum of 30 minutes was allocated to census each block; actual counting time averaged 19.3 ± 6.9 minutes (0.038 min/ha). No time limit was placed on counting the three high density areas, but search effort was similar to the blocks (0.034 min/ha). Lower boundaries of each unit were flown first, at about 1,570 m, and then the unit was searched upslope at 75-100 m intervals. Airspeed during census was about 40-70 mph using an Aerospatiale A-Star 350D helicopter. The census team included the pilot, two observers, and one navigator—the latter responsible for locating units, directing the pilot along block boundaries, and timekeeping.

The population total was calculated using Jolly's (1969) method for unequal sized sample units, as outlined by Norton-Griffiths (1978:72). This approach, applied to the medium and low density strata, uses the density of animals rather than the number observed per block to produce the estimates. This was necessary because of the variation in block size; we were only modestly successful in producing uniform 500 ha census blocks that could be recognized from the air. The counts for the three high density areas (stratum 1) and the calculated total for Klahhane Ridge (stratum 4) were added, without variances, to the estimates for strata 2 and 3, a move analogous to "stratifying out large herds" (Norton-Griffiths 1978:84).

Aerial census is known to underestimate the actual numbers of animals present (Caughley 1977, Norton-Griffiths 1978). Consequently, the "index-manipulation-index" (IMI) method of population estimation (Caughley 1977) was used during the 1981-83 period of goat removal to estimate a bias error for the overall census. Population size was estimated from an index of density (helicopter counts) before and after a known number of animals was removed by trapping from the Klahhane Ridge (census stratum 4). Counting procedures were generally similar to those described above; except, a Bell Jet Ranger III helicopter was used in 1981, and a Hughes 500D in 1982. Two censuses (one morning, one evening) were made before and two after the goats were removed in 1981 to test the "repeatability" of the counts. One count was made before and one after the removals of 1982 and 1983. Flights were made during periods of maximum daily goat feeding activity (Stevens 1979).

Results and Discussion

Establishing a bias error. The IMI method requires that goat habitat use and avoidance behavior remain constant, and that corrections can be made for mortality occurring between counts. Studies have shown that goat use of open vegetation types on Klahhane Ridge is consistently high during the late June-mid-July periods of IMI census (Stevens 1979). Daily field observations made each year between the flights suggested that no major changes occurred in goat use of vegetation types. Goats may learn to seek cover if approached frequently by aircraft, and helicopters were used to remove trapped goats. However, pilots were instructed to fly directly from the low elevation staging area to the capture site, thus avoiding adjacent goat habitat. Observations of goat behavior, plus the continued successful trapping suggest that the effects of local helicopter traffic were minimal. Mortality of neonates occurred between IMI censuses and this was corrected as described below. We consider that the conditions necessary to use the IMI method were met to the extent that a useful bias error was generated.

Counts and population estimates for the Klahhane unit are summarized in Table 1. Only two age classes of goats could be distinguished reliably from the air, young-of-the-year and all older animals. Counting time (mean ± SD) was 88 ± 16 minutes for the eight flights. Overall repeatability of the 1981 attempts was high: total counts varied by only two goats between

TABLE 1. Mountain goats observed during helicopter counts of Klahhane Ridge, 1981-83.

Year	Date Time	Number of Goats: Adults and Yearlings	Young	Total	Total Goats Removed	Total Population[2]
1981	*Pre-removal*					
	24 June 0718-0828	130	24	154		229(198 ± 31)[1]
	26 June 1752-1909	135	17	152		
					52(50 + 2)[1]	
	Post-removal					
	16 July 1833-1955	103	14	117		171(148 + 23)
	17 July 0648-0804	95	17	112		
1982	*Pre-removal*					
	23 June 0626-0819	97	28	125		176(137 + 39)
					51(41 + 10)	
	Post-removal					
	19 July 0645-0820	68	21	89		126(96 + 30)
1983	*Pre-removal*					
	21 June 0628-0822	68	22	90		147(111 + 36)
					52(39 + 13)	
	Post-removal					
	19 July 0637-0825	44	8	52		85(72 + 13)

[1]Total (adults and yearlings + young).
[2]Adults and yearlings calculated using IMI census.

pre-removal flights, and five goats between post-removal flights. Differences within age classes were greater: the number of young observed varied as much as seven between pairs of flights, adults and yearlings, as much as eight. Neither morning nor evening counts produced consistently better results; however, morning counts were preferred because of better light conditions and calmer air.

Ground observations of tagged females showed that some mortality of young occurred during the 22 days between the 1981 censuses (Stevens 1981, personal communication). A less biased estimate should result from using only the adults and yearlings observed during aerial census, avoiding the effects of neonatal mortality. The numbers of young were estimated separately from the observed ratios of young to adults. Calculations follow Caughley (1977:47) and are presented in detail elsewhere (Aho *et al.* 1984). Fifty-two goats (50 adults and yearlings, 2 young) were removed from the subpopulations 30 June-8 July. The mean numbers of adults and yearlings observed during the pairs of flights were used in the calculations, even though we suspected goats were somewhat more disturbed during the second flight of each pair. The adult and yearling pre-removal population was calculated as 198 goats; post-removal, 148.

Mean young/adult-and-yearling ratios for pre-removal and post-removal counts were 0.155 and 0.157, respectively. The higher post-removal ratio is reasonable, because females with young at heel were not removed in proportion to their occurrence in the population. The estimate of the total pre-removal population using the IMI technique is 229 (198 adults and yearlings + 31 young); postremoval, 171 (148 + 23). Similar calculations were used to determine population size in 1982 and 1983 even though neonatal mortality appeared to be very low (Table 1).

Some approximate 90 percent confidence limits (CL) were calculated for the IMI pre-removal estimates under the assumption that the counts represented Poisson random variables (Eberhardt 1982:735, equation 6). The CL were calculated for the adult and yearling segment of the population. The estimates with CL were: 198(133-326), 137(97-220), 96(68-156) for 1981-83, respectively. The actual number of goats observed was substituted for the calculated lower limit. The CLs declined somewhat over time as

an increased proportion of the population was removed (Eberhardt 1982). Nevertheless the calculated limits remained very broad.

Calculations using the 1981 count of adults and yearlings suggest a bias error of 0.33. This represents a measure of census efficiency, the difference between the goats observed and those actually present, and calculated as 132.5/198 or 0.67 of those present were observed. Similar calculations suggest bias errors of 0.29 and 0.39 for 1982 and 1983, respectively. The 3-year mean observability of 0.66 was used to adjust the 1983 overall census.

The main census was conducted in seven early morning flights from 21-31 July 1983. Total census time (including travel between counting blocks and the Hurricane Ridge staging area) was 18.2 hours.

A total of 396 goats (324 adults, 72 kids) was counted in strata 1-3 during the main census (Table 2, Figure 1). As expected, counts in the medium density stratum were highly variable. Observed densities in two blocks exceeded those in the known high density stratum.

The average 66 percent census efficiency from Klahhane Ridge was used to produce a more accurate estimate (*i.e.,* nearer the true total) by initially multiplying the number of goats observed in each block of strata 1-3 by 1.52 (the reciprocal of 0.66). The estimate of 66 percent observability is conservative; the south and southeast portions of the census zone support more shrub and forest cover than Klahhane, and census efficiency is surely lower. Johnson (1983:68) used ratios of marked to unmarked goats observed during an August 1981 helicopter count to calculate a census efficiency of 63 percent for the Iron Mountain-Charlia Lakes area in the northeast Olympics (within the census zone used in this study).

The estimated goat population for strata 2-3 ($\hat{Y}_{2-3}$) was calculated as:

	$\hat{Y}_h$	$Var(\hat{Y}_h)$	Number of blocks
Stratum			
2 (low density blocks)	35	491	6
3 (medium density blocks)	882	28,875	28
Total	917	29,366	34

The standard error ($\hat{Y}_{2-3}$) is $\sqrt{Var\ (\hat{Y}_{2-3})}$ or 171 goats. When the 173 goats in the high density total count units are added, $\hat{Y}_{1-3}$ is 1090. Finally, the Klahhane estimate (stratum 4) of 85 goats can be added to give $\hat{Y}_{1-4} = 1175 \pm 171(SE)$ for the population in the census zone during July 1983. Detailed calculations are presented in Aho *et al.* (1984). This estimate is substantially greater than those made earlier. As mentioned, observed goat densities in two blocks of the putative medium density stratum exceeded those in the known high density stratum (Chimney Peak, n = 52; Dana-Wilder, n = 45). These rude surprises added considerably to the standard error. If these two blocks are included as part of the known high density stratum, for illustration, and all calculations are repeated, $\hat{Y}_{1-4}$is 1,036 goats with the standard error reduced to ± 111.

Armed with the results of this first census, the precision of future counts could be improved by restratification and by calculating bias errors for different vegetation types. However, given the precipitous terrain, the highly clumped distribution of mountain goats, and the observation that block counts have inherently larger sampling errors than transects (Norton-Griffiths 1978), future counts can also be expected to return large standard errors. This may be particularly true in the Olympics, where goats are still colonizing the range and many subpopulations have probably

TABLE 2. Area sampled and mountain goats counted in the Olympic Range, July 1983.

Stratum	Area(ha)	No. Blocks	Area Sampled	No. Blocks Sampled	Goats Counted	Adjusted Goat Numbers[1]
(1) Known High	5,071	—	5,071	—	114	173
(2) Low Density	13,135	26	2,847	6	5	7.6
(3) Med. Density	29,860	59	14,251	28	277	421
(4) Klahhane	1,997	—	1,997	—	—	85

1. Numbers observed x 1.52 for strata 1-3. Stratum 4 estimated by IMI, see text.

not yet achieved ecological carrying capacity. Wherever subpopulations grow rapidly, the information on density needed to produce census strata is soon outdated. For all its limitations, the census indicates that the goat management problem facing the National Park Service is very likely larger than anticipated initially.

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Influence of Stream Gradient on Standing Stock of Brook Trout in the Snowy Range, Wyoming

Abstract

Gradient and other instream habitat variables were assessed for their influence on brook trout (*Salvelinus fontinalis*) abundance in small streams where brook trout were the only fish species present. Brook trout occurred throughout the gradient-range studied (0.4-9.2 percent), but increased gradient had a negative influence on abundance. Gradient, width to depth ratio, mean depth, and mean width accounted for 68.8 percent of the variation in brook trout abundance among the 24 study reaches.

Introduction

Stream gradient is believed to have a negative influence on the abundance of brook trout (*Salvelinus fontinalis*) in small Rocky Mountain streams. The relation between gradient and abundance has been evaluated, but only for brook trout in the presence of other salmonids. Brook trout have been observed to be most abundant in low gradient stream reaches and cutthroat trout (*Salmo clarki*) in high gradient reaches (Bachmann 1958, MacPhee 1966, Griffith 1972). Gibson (1978) made a similar observation in streams containing brook trout and Atlantic salmon (*S. salar*): brook trout were most abundant in pools and salmon in areas with higher water velocity. Observations on resource partitioning have been made in streams where rainbow trout (*S. gairdneri*) and brown trout (*S. trutta*) occurred with brook trout (Nyman 1970, Cunjak and Green 1983).

The hypothesis that brook trout biomass is related to stream gradient in small Rocky Mountain streams was tested in the Snowy Range of Wyoming, where only brook trout occur in many streams. Because confounding influences of possible competition with other fish species did not occur, we were able to test whether the relation was due simply to habitat selection by brook trout.

Study Area and Methods

We evaluated 24 reaches in 13 streams in 1984; all reaches were at an elevation of 2,800 to 3,200 m and there were no nearby beaver ponds. The streams were in coniferous forest or subalpine habitats. Gradients in the reaches studied ranged from 0.4 to 9.2 percent. All streams had flow patterns typical of those in streams of the Rocky Mountain Region: flows were low from late fall until spring (May to July), when peak runoff occurs due to snowmelt.

Study reaches were 65-85 m long. Gradient of each stream reach was measured with a transit level and rod or a clinometer. Within each reach, we measured width, depth, and substrate along transects at 5-m intervals, using the procedures of Platts *et al.* (1983). We used a portable direct current electrofishing unit, isolated the upper and lower limits of each reach with block nets, and performed three consecutive electrofishing passes in each reach. Brook trout abundance in each reach was estimated by the method described by Zippin (1958).

Relations between independent variables and brook trout abundance were analyzed by one-way analysis of variance, the Newman-Keuls test, and stepwise-multiple regression (Nie *et al.* 1975).

Results

The 24 stream reaches were segregated into three gradient classes for analysis (Figure 1): low (0.4-1.8 percent, $n = 8$), moderate (2.0-5.0 percent, $n = 10$), and high (6.8-9.2 percent, $n = 6$). Standing stock differed significantly among the three gradient classes (ANOVA, $F = 4.43$, $P = 0.025$, $df = 23$). The average standing stock of brook trout was 40.5 kg/km (SD = 24.7) in low gradient, 24.7 kg/km (SD = 12.9) in moderate gradient, and 14.1 kg/km (SD = 5.2) in high gradient. Paired comparisons of the mean standing

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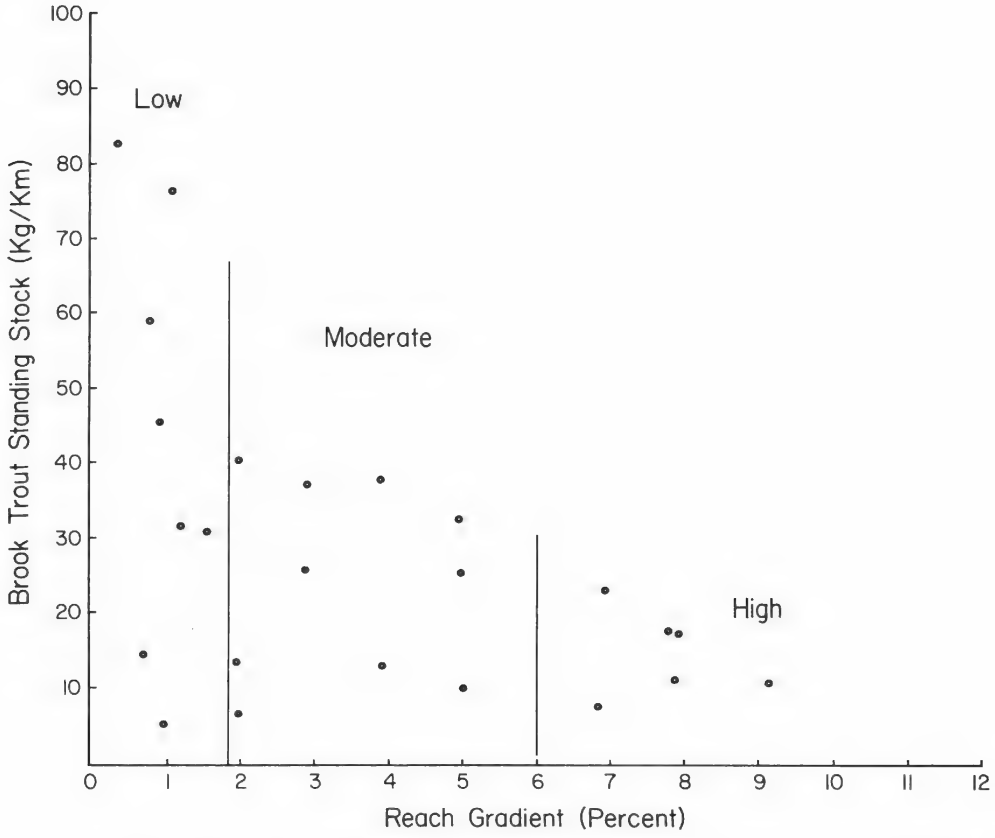

Figure 1. Relation between stream gradient and brook trout standing stock for 24 stream reaches in the Snowy Range, Wyoming, 1984.

stock between gradient classes, based on the Newman-Keuls test, yielded significant differences ($P \leq 0.10$) among all three gradient classes.

The amount of variation in standing stock within each gradient classes declined with increasing gradient. The coefficients of variation for reaches at different gradients were 61.1 percent (low gradient), 52.2 percent (moderate), and 36.6 percent (high).

Stepwise multiple regression analysis indicated that stream gradient accounted for 25.5 percent of the variation in standing stock among the 24 study reaches. In addition to gradient, the width to depth ratio, mean depth, and mean width over a stream reach cumulatively accounted for 68.8 percent of the variation in brook trout standing stock among the 24 study reaches. The multiple regression equation for this relationship was

$$S = -9.88 - 3.43G + 1246.8W/D + 12.28D - 321.5W \ (P = 0.0001),$$

where S = kilograms of trout per kilometer of stream; G = gradient over the stream reach; W/D = width to depth ratio; D = mean depth (m); and W = mean width (m). This equation indicated that instream habitat variables accounted for variation in brook trout standing stock within the range of gradients (0.4-9.2 percent) analyzed.

Discussion

The results of this study confirmed that gradient influences the standing stock of brook trout, even in the absence of other fish species. Although brook trout occurred throughout the gradient range studied, they were about three times more abundant in low gradient than in high gradient reaches. As gradient increased, variation in standing stock decreased, an indication that other habitat variables had a stronger influence on standing stock at low than at high gradients. Gradient appeared to limit the upper level of standing stock of brook trout in streams of the Snowy Range of Wyoming.

High stream gradient appears to have a similar negative influence on brown trout and rainbow trout. Kennedy and Strange (1982) found brown trout to be limited to areas of low gradient, and Hermansen and Krog (1984) found brown trout density in small lowland streams to be negatively correlated with gradient. Such a situation may lead to competition between brook trout and brown trout in streams where both species occur (Cunjak and Green 1983). In low-gradient habitat, brook trout have been shown to dominate rainbow trout, thus providing a species advantage for brook trout when preferred habitat is limited (Cunjak and Green 1984).

Some salmonids, such as cutthroat trout (Bachmann 1958, MacPhee 1966, Griffith 1972) and Atlantic salmon (Gibson 1978), appear to select for high gradient reaches and to segregate themselves from brook trout when the species live in the same stream. This partitioning of space probably reduces competition between brook trout and these salmonids.

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Activity Pattern of a Pair of Nesting Flammulated Owls (*Otus flammeolus*) in Idaho

Abstract

A single flammulated owl (*Otus flammeolus*) nest was monitored during late incubation and early nestling period to determine the pattern of nest visits by foraging adults. Visits to the nest by adults began each evening 10 to 30 minutes after sunset and ended during the hour before sunrise. The foraging adults were most active in early evening and just before dawn, although they visited the nest throughout the night. The number of nocturnal nest visits increased linearly during the nestling period from 22 visits per night recorded prior to hatching, to 97 visits per night when the oldest of three young was 15 days old. This increase was accomplished by shortening the intervals between delivery bouts during the middle of the night. There was no evidence of diurnal foraging.

Introduction

A complete understanding of the role a species plays in a community requires information on use of space, food, and time. Nesting flammulated owls (*Otus flammeolus*) occupy stands of ponderosa (*Pinus ponderosa*) or Jeffrey pine (*P. jeffreyi*) in the Transition zone of western North America (Marshall 1939, Bull 1978, Bloom 1983, and others). Specific characteristics of sites used for nesting can not be defined from current information (Bull 1978, Richmond *et al.* 1980). Casual observations indicate flammulated owls are nocturnal and insectivorous (Johnson and Russell 1962, Johnson 1963, Marshall 1939). As such, the species appears to exploit resources utilized by few other nocturnal vertebrates (bats and Caprimulgiforms).

To define the role flammulated owls play in a coniferous forest community, the timing of the owls' daily foraging activity, species composition of its prey, and numbers of prey consumed must be determined. Although limited, data collected at a single flammulated nest in 1982 quantitatively describe the daily activity period of a nesting pair and suggest the magnitude of prey numbers consumed by the owls.

Study Area

On 16 June 1982 I found a flammulated owl nest cavity 1.5 m high in a 2.5 m ponderosa pine stub. The nest was located on the Boise Basin Experimental Forest, Boise County, Idaho, in an unharvested stand of old growth ponderosa pine—Douglas fir (*Pseudotsuga menziesii*) forest about 25 m from a seven-year-old clearcut. The approximately 35 ha forest stand varied in structure from open, overmature, ponderosa pine with little understory to a multilayered, closed canopy of mixed ponderosa pine and Douglas fir, to mature timber with a dense understory of ninebark (*Physocarpus spp.*). Based on two 1000m² plots located within 200 m of the nest, Pregitzer (1983) classified the stand as *Pseudotsuga menziesii/Spireae betulifolia—Pinus ponderosa* phase (Steele *et al.*1981). Forest cover for trees over 10 cm dbh was 60 percent ponderosa pine and 40 percent Douglas fir, averaged 580 live trees per ha and 40 snags per ha. Sixty trees per ha were over 35.6 cm (14 in) dbh and included 50 trees per ha over 30.5 m (100 ft) with the largest tree measuring 136.5 cm (53.7 in) dbh and 49.1 m (161 ft) tall.

Immediately around the nest the overstory was overmature ponderosa pine with an understory of Douglas fir saplings. The nest cavity faced a clearing approximately 7 m diameter. Bull (1978) described four nest sites, all in similar two or three layered oldgrowth ponderosa pine stands.

Methods and Results

Prior to 14 July, I visited the nest only at dawn or during daylight. During 20 visits between 16 June and 14 July an adult owl was always present within the nest cavity. At 0807 on 14 July and at 1400 on 15 July, an adult was not present. It was not apparent what role male and female owls played in incubation.

On 30 June one egg hatched, and one unhatched egg was visible beneath the brooding bird. On 5 July the young owls called with weak peeping sounds. On 13 July one young began clapping its bill when I visited the nest. On 14 July, three downy young were visible, each with patches of emerging darker contour feathers.

In an attempt to determine diets, I photographed prey deliveries during the first one-half hour of activity on two nights (14, 15 July). Seven photographs had recognizable prey; two noctuid moths (likely *Catocala* spp.), a camel cricket (likely a predominantly ground dwelling form in the family Gryllacrididae), two moth larvae (one possibly *Catocala* spp.), an unidentified moth, and an unidentified beetle or spider.

Using a Bacharach 24-hour clock and event recorder I monitored adult nest visits from 27 June to 14 July 1982. The event recorder, triggered by a small perch attached to an electric switch placed across the lower side of the cavity entrance, recorded the time of day for all nest visits. Observations at this nest and two boreal owl (*Aegolius funereus*) nests (author's unpublished data) indicate the nest cannot be entered, or a prey delivery made, without triggering the perch. The recorder is not activated when an owl leaves the cavity.

Observations and photographs indicated that the adult owls did not enter the cavity during feeding visits, but perched at the entrance and placed only their head into the cavity. Feeding visits usually lasted less than five seconds. Because visits were brief, and the owls did not enter the cavity, only one mark was registered on the event recorder per visit. Each mark on the recording paper was therefore considered a nest visit. The total number of events for any one night, however, should be considered conservative since two visits within a minute of one another may not be distinguished as two records. This assumption was especially important late in the nesting period when both adults were foraging and feeding the young.

The clock appeared to have run slowly the night of 30 June. Although the number of events could be counted, the events could not be assigned a particular time for that night. Since the recorder was not attended from 2-5 July records on the graph were too dense to count accurately but the earliest evening record and latest morning record for this period were ascertained.

The owls generally showed a burst of nest visits 10-30 min. after sundown, which lasted 30-40 min., and again 45-75 min. just before dawn (Figure 1). During 17 days of recording, only one visit occurred during daylight hours. Early in the nesting period, when fewer visits were recorded, the events throughout the night were clumped, with visiting bouts followed by 15 to 90 min. breaks. Eleven days after hatching (on 10 July), 64 visits were recorded during the night with six breaks of 15 min or longer and one break over 30 min. For five of these seven breaks, at least three deliveries occurred in the 15 min preceding or following the break.

To evaluate the distribution of nest visits throughout the night, I recorded the number of visits by 30 min periods over 13 days (excluding 30 June and 2-5 July, Figure 1). A test of the hypothesis that nest visits were distributed uniformly throughout the night was rejected ($x^2 = 82.65$, $df = 16$, $p < 0.0001$) due to the concentrated activity in early evening and dawn. When an hour of activity at dawn and dusk were excluded, a chi-square test was not significant ($X^2 = 18.91$, $df = 12$, $p = 0.091$).

The time of onset and cessation of activity were consistent over the 17-day recording period (Figure 1). Time of the first visit each evening varied by 41 min but 10 of 13 recorded first visits began within 20 min (2140-2200). The time when activity commenced each morning varied by 51 min, however, 8 of 12 recorded final visits occurred between 0540-0600 (Figure 1).

Total number of nest visits each night changed through the nesting period (Figure 1). While feeding the brooding adult and young during the early nestling stage, the foraging adult presumably uses cues from its dependents to adjust the feeding rate to their needs (Welty 1975:341-342). Later in the nesting cycle, both parents feed the developing young; the incubating adult will begin to assist in foraging when food being supplied fails to meet its needs. Johnson and Russell (1962), Marshall (1939), and my photographs, indicate flammulated owls are insectivorous and consequently consume prey of a relatively consistent size class. Therefore, the pre-hatching total nightly visitation should indicate the food requirements of the brooding owl (assuming prey is delivered at each visit). The rate of increase in the number of deliveries each night

should reflect the growing food requirements of the young.

The number of nest visits showed a significant linear relationship ($y = 28.4 + 3.7x$) with the period of the nesting cycle. For the linear regression analysis, the night prior to the night the first egg hatched was designated day 1 (28 June) and the nesting cycle numbered sequentially. A random distribution of residuals, a high r^2 (0.84), and significant F test on the overall regression ($p < 0.01$), indicate that the relationship was linear over the period studied. A 95 percent confidence interval (2.58 to 4.88) for the slope, indicates an average rate of increase between three and five visits each night, or about one visit per nest occupant per night.

The number of nocturnal nest visits progressively increased by shortening the intervals between feeding bouts during the middle night and extending the periods of feeding activity in evenings and mornings. The rate of visits during the first and last 30 min of the active period did not change through the nesting period (Figure 1).

Seven photographs taken on two nights showed one insect being carried at each visit. If this is the norm, an incubating owl requires about 22 insects a day as indicated by the pre-hatching visitation rate (presuming the incubating owl did not leave the nest to forage). Over a 49-day incubation and nestling period, the nest occupants consumed an estimated 2314 insects. The estimate assumes 22 insects a day for the incubating owl during 25 days of incubation (Eckert and Karalus 1974) and estimates the consumption by nest occupants after hatching based upon the regression equation and a 24-day fledging period (I limited the level of consumption to that of day 20 for days 20 to 24). My estimate of insect consumption probably overestimates consumption late in the nestling period, underestimates that of the incubating owls, and provides no estimate of consumption by foraging owls. However, it indicates the magnitude of insects one nest of flammulated owls may consume in 49 days.

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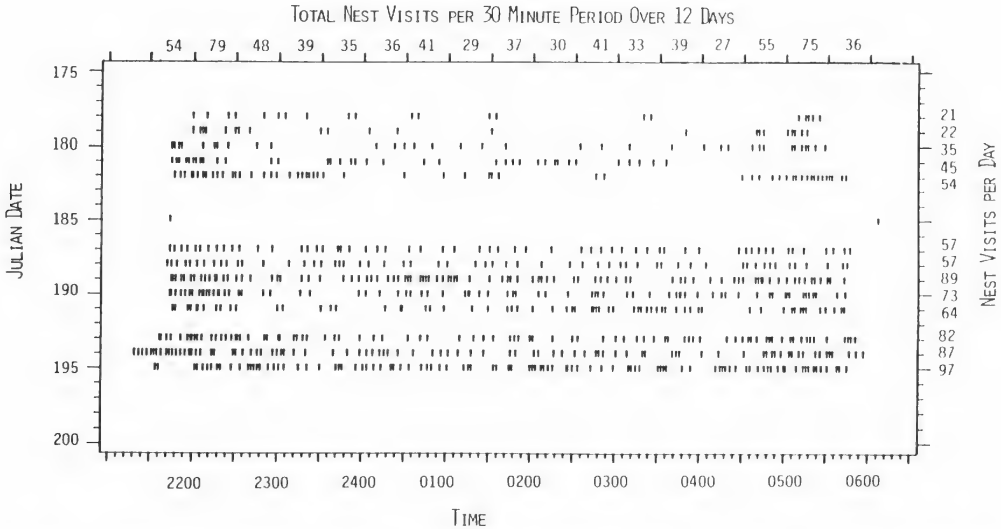

Figure 1. Nocturnal activity pattern of a pair of nesting flammulated owls recorded at a nest cavity in Boise County, Idaho. On 30 June (181) a slow clock prevented recording accurate times of activity for that night. Because the recorder was not serviced from 2-5 July (183-186) only the earliest and latest records for this period could be used. On 11 July (192) a recorder malfunction prevented recording of activity.

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Radiation Dosimetry on Revegetated Uranium Mill Tailings in Western South Dakota

Abstract

Measurement of gamma radiation using thermoluminescent dosimeters on three uranium mill tailings areas and a control area showed exposure rates below ground depended on the amount and type of soil covering. Covering tailings with 30 cm of shale and 60 cm of topsoil reduced gamma radiation exposure belowground to rates similar to the control area. Soil covering of 30 cm was adequate to reduce gamma radiation exposure rates aboveground to background levels. Gamma exposure rates to small mammals were correlated to measurements belowground near the surface. Gamma radiation exposure to small mammals inhabiting uranium mill tailings exceeded standards recommended for the general public.

The waste materials from uranium milling processes (tailings) contain low amounts of radioactive materials in the U-238 decay series. To assess the health risks from these radioactive materials, it is necessary to determine the amounts of nuclear waste materials in soils and vegetation on these sites, and the radiation exposure to fauna, including humans.

Studies have been conducted to evaluate the levels of radiation exposure to small mammals (Halford and Markham 1978, Gano 1979) and waterfowl (Halford *et al.* 1982) inhabiting spent nuclear fuel waste disposal sites. However, these sites contain nuclear reactor by-products, higher in radioactivity than uranium mill sites. Information pertaining to the radiation received by small mammals inhabiting uranium mill tailings sites is lacking. This study compares the levels of gamma radiation exposure to small mammals and their environment on uranium mill tailings to background levels on a control site.

Study Area and Methods

The uranium mill tailings immediately west of Edgemont, South Dakota were selected for this study. The mill has been inactive since 1972 and is scheduled for decommissioning.[1] Four sites were selected for study. Sites 1 and 2 were uranium mill tailings covered with 30 cm of topsoil, with established vegetation dominated by crested wheatgrass (*Agropyron cristatum*) and yellow sweetclover (*Melilotus officinalis*) seeded in the fall of 1973 and spring of 1974, respectively. Site 2 differed from site 1 in that background gamma scan counts measured 1 m aboveground indicated a higher level of gamma radiation on the site. Site 3, also uranium mill tailings, was covered with 30 cm of shale and 60 cm of topsoil with the dominant species of vegetation being crested wheatgrass, western wheatgrass (*Agropyron smithii*), and yellow sweetclover all seeded in 1978. The control site was a pasture located west of the mill, dominated by crested wheatgrass, red threeawn (*Aristada longiseta*), and sand dropseed (*Sporobolus cryptandrus*).

On each site, a grid of 77 (7 x 11) Sherman collapsible small mammal live-traps (23 x 9 x 8 cm) spaced at 7 m intervals, was established. Trapping was conducted monthly from June through September of 1981 and April through September of 1982. The goal was to catch as many small mammals as possible, attach dosimeters and recapture these animals at a later date. Because trapping success was poor on the control site during the first trapping period, an additional 30 traps were set adjacent to the control site. All traps were baited with rolled oats mixed with peanut butter and were opened five consecutive nights at monthly intervals. Animals captured on all sites were toe-clipped for identification and age, sex, weight, and species were recorded.

During 1981 all animals captured were anesthetized and surgically implanted (subcutaneously) with a waterproof packet containing two, 0.32 x 0.32 cm thermoluminescent dosimeters (TLD's) (Halford and Markham 1978, Gano 1979). A different technique was used during

[1]Silver King Mines, Inc., manages the site for the Tennessee Valley Authority.

1982; TLD's were attached to both ears of the animals with two Monel metal tags. Each TLD chip was affixed to the ear tag by a piece of 0.32-cm heat-shrink tubing. The animals were then released at the capture location. Animals with TLD's recaptured after 30 or more days had the old TLD's replaced with new ones and the animal was released again. No new TLD's were put on small mammals in September of 1981.

Gamma radiation on the sites was measured by sets of TLD's attached to wooden rods at 80, 60, 40, and 20 cm belowground and at 0, 10, 20, 40, 60, and 80 cm aboveground. One set of TLD's was placed at the center of each small mammal trap grid and one set of TLD's was placed at the center of each quarter of the small mammal grid. These TLD's were in the field 30 days. Exposed TLD's were placed in lead containers while in the field and during storage.

The TLD's, which had been calibrated with a Ra-226 source were initially selected to be within ± 10 percent error due to chip variability and error associated with the reading. All TLD's exposed in the field and some TLD's stored in a lead container in the laboratory were sent for analysis. Analyses were conducted by Eberline Laboratories.[1] Exposure levels of TLD's kept in the laboratory were subtracted from those exposed in the field to account for irradiation during shipping and handling. TLD exposure data are given in milliRoentgens per day (mR/day). Radiation exposure data from these TLD's are only representative of gamma and some high-energy beta forms of radiation. Differential shielding by the techniques used for attaching TLD's was not of consequence since most gamma radiation easily passes through up to 1.0 inches of iron (U.S. Department of Health, Education and Welfare 1970).

Radiation exposure data on all treatments were analyzed separately for aboveground and belowground in a split-plot design (Steel and Torrie 1960). Sites were considered whole plot effects and depths were treated as subplot effects. Since the interaction of site by depth for the belowground analysis was significant ($P < 0.01$), separate one-way analyses of variance were performed at each depth. Differences among exposure rates belowground for sites at each depth were evaluated using Dunnett's T3 method for non-homogeneous variances (Dunnett 1980). Significant differences from the aboveground procedure were evaluated using Tukey's multiple comparisons method for homogeneous variances (Steel and Torrie 1960). Radiation exposures to the small mammals were analyzed by two-way analysis of variance for species and sites. Tukey's method was used to determine where differences occurred. Probability level for all tests was $\alpha = 0.05$.

Results

The relationships of gamma radiation estimates from TLD's placed in the field are displayed in Figure 1. Belowground exposure rates suggest a decrease in radiation exposure as the distance between tailings materials and the TLD's increased. Estimates of gamma radiation at the various heights aboveground were variable. Exposure rates aboveground and belowground on site 2 remained relatively constant. Radiation estimates from site 3 and the control site increased aboveground versus belowground.

Belowground radiation rates differed significantly among sites, depths, and site by depth (Table 1). Analyses of radiation exposure estimates 80 cm belowground indicated that higher levels occurred on site 1 compared to the other sites. Gamma exposure estimates from site 2 were higher than those from the control site, but not different from estimates from site 3. Site 3 and the control site were not significantly different. At 60 cm belowground, gamma radiation estimates from site 1 were not different from site 2 estimates; but were greater than those from site 3 and the control site. Gamma radiation estimates from site 2 were higher than those from the control site, but not different from those from site 3. Site 3 and the control site were not different. Estimates of radiation exposure 40 cm belowground indicated no differences between site 1 and site 2, but site 1 had higher estimates than did site 3 and the control site. At 20 cm belowground, no statistical differences were found among the sites.

Aboveground radiation exposure estimates were significantly higher on site 2 versus sites

[1]The use of trade, firm, or corporation names in this publication is for the information and convenience of the reader. Such use does not constitute an official endorsement or approval by the U.S. Department of Agriculture of any product or service to the exclusion of others which may be suitable.

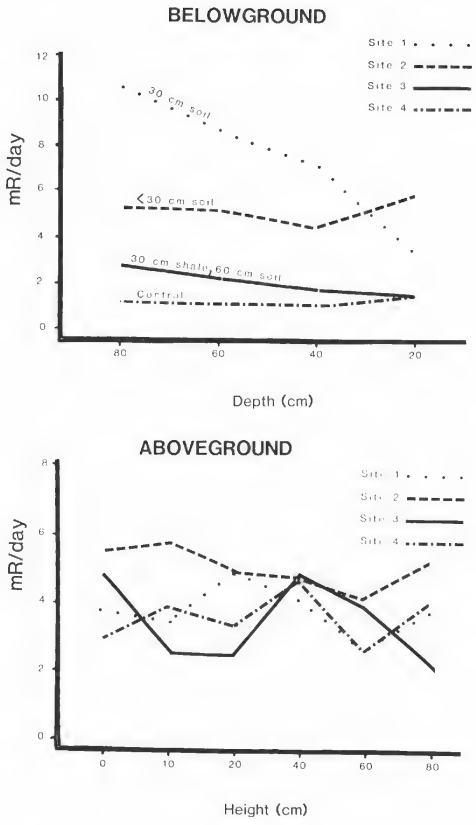

Figure 1. Belowground and aboveground estimates of gamma radiation from three uranium mill tailing sites with topsoil and/or shale covering and a control site. Plotted values are means, n = 5.

1, 3, and the control site (Table 1). Estimates of radiation exposure among the heights aboveground were not statistically different.

Small mammals inhabiting the four sites were exposed to variable levels of radiation (Table 2). Differences in estimated radiation exposure were found among sites, but not among species. Averaged across species, small mammals on site 2 were exposed to higher levels of radiation than on the other three sites ($P < 0.001$). Radiation received by the individual species averaged across sites were not different ($P = 0.06$) which may have been related to the limited sample size. Estimates of radiation received by the small mammals inhabiting all sites was positively correlated with averaged gamma radiation estimates measured at ground level. For all species together $r = 0.68$, for western harvest mice (*Reithrodontomys megalotis*) $r = 0.50$, and for prairie voles (*Microtus ochrogaster*) $r = 0.86$. There were not enough deer mice (*Peromyscus maniculatus*) captured to get meaningful correlations of exposure rates across sites. Higher correlations of 0.97, 0.78 and 0.86 were found for exposure rates 20 cm below ground for all species, western harvest mice and prairie voles, respectively. Mean gamma exposure to the small mammals on each site was less than the exposure rates measured either aboveground or belowground.

Discussion

Measurements of belowground radiation exposures suggested some differences between sites with supposedly similar soil covering and vegetation (site by depth interaction belowground). These differences were attributed to the uneven spreading of topsoil over mill tailings on site 2 versus site 1. Near the center of the grid area on site 2, the top soil depth was as shallow as 10 cm. Thus, at least some TLD's at all depths belowground were in the raw tailings materials. Covering the mill tailings materials with 30 cm of shale and 60 cm of topsoil reduced belowground estimates of radiation exposure in this study to rates not different from those at the control site (background rates) down to 80 cm.

An evenly spread soil covering of 30 cm over uranium mill tailing materials reduced aboveground radiation exposure to levels not different from background. Schaiger (1974) indicated 61 cm of soil was needed to reduce gamma exposure to natural background levels. However, the fact that these data were highly variable may have obscured some differences. On other uranium mill tailing sites, gamma counts at 1 m aboveground varied between 2.2 mR/day at Gunnison, Colorado, to 7.5 mR/day near Rifle, Colorado, when covered with 15 to 30 cm of soil. In this study, gamma radiation measurements for sites 1 and 2 averaged 4.3 mR/day aboveground. Gamma radiation counts on uranium mill tailing sites with no soil covering varied from 17.1 mR/day at Tuba City, Arizona, to 31.7 mR/day at Mexican Hat, Utah (unpublished data, U.S. Dept. Energy Uranium Mill Tailings Project Office, Albuquerque, New Mexico).

TABLE 1. Mean ±SE radiation estimates (mR/day) from three uranium mill tailings sites covered with topsoil and/or shale and a control site.[1]

	Site 1 30 cm topsoil	Site 2 30 cm topsoil	Site 3 30 cm shale & 60 cm topsoil	Control
Belowground				
80 cm	10.6 ± 0.2[a]	5.3 ± 0.6[b]	2.8 ± 0.3[b,c]	1.2 ± 0.5[c]
60 cm	8.6 ± 0.9[a]	5.2 ± 0.7[a,b]	2.2 ± 0.2[b,c]	1.0 ± 0.2[c]
40 cm	7.1 ± 0.8[a]	4.4 ± 0.7[a,b]	1.6 ± 0.2[b]	1.0 ± 0.1[b]
20 cm	3.3 ± 0.5	5.8 ± 1.4	1.5 ± 0.2	1.4 ± 0.2
Aboveground[2]				
$\bar{x}$	3.5 ± 0.3[b]	5.5 ± 0.5[a]	3.4 ± 0.4[b]	3.7 ± 0.5[b]

[1]Means followed by superscripts with different letters across rows are different ($P \leq 0.05$) based on Dunnett's T3 method for nonhomogeneous variances belowground and Tukey's w-procedure aboveground.
[2]No differences were found among heights aboveground so only site means are presented.

TABLE 2. Gamma radiation (mean ± SE)[1] in mR/day to small mammals inhabiting three uranium mill tailings sites and a control site in South Dakota.[2]

Species	Uranium Mill Tailings Site 1	Site 2	Site 3	Control	All treatments averaged
Western harvest mice	1.49 ± 0.49 (8)[2]	3.12 ± 0.36 (6)	1.69 ± 0.48 (3)	0.63 (1)	2.02 ± 0.31 (18)
Deer mice	1.26 ± 0.40 (8)	0.51 (1)	—	0.53 ± 0.39 (2)	1.06 ± 0.31 (11)
Prairie voles	0.45 (1)	4.19 ± 1.64 (4)	0.32 ± 0.34 (8)	0.19 ± 0.04 (12)	0.87 ± 0.38 (25)
All species averaged	1.32 ± 0.29 (17)[a]	3.27 ± 0.66 (11)[b]	0.69 ± 0.22 (11)[a]	0.26 ± 0.06 (15)[a]	1.30 ± 0.22 (54)

[1]Means with different letters as superscripts are significantly different at $P \leq 0.05$.
[2]Number in parenthesis is the sample size.

Small mammals in the field received lower rates of radiation exposure than were observed aboveground on the study sites. This indicates that the animals spent at least part of the time in situations where radiation rates were less than measured on the four sites. Undoubtedly TLD's placed at ground level in the field received some gamma radiation from both below- and above ground. The relationships of 20 cm belowground and ground level exposure rates to small mammals exposure rates would indicate the primary source of radiation exposure to small mammals inhabiting mill tailing sites was the uranium mill tailings. All three mammal species in this study are active at night and nest on or near the surface (Burt and Grossenheider 1964) and, with the exception of prairie voles, are active at night (Leichleitner 1969). Thus, the small mammals were not exposed to some of the external sources of radiation (*i.e.* solar) that were measured with the stationary TLD's at or aboveground. Higher gamma exposure rates belowground compared to small mammals exposure rates indicates some degree of attenuation of gamma radiation from the mill tailing by the soil covering.

Information to compare gamma exposure rates to small mammals on other uranium mill tailing sites is lacking. However, if one assumes

that humans would receive doses similar to the small mammals, some comparisons can be made. The U.S. Department of Health, Education and Welfare (1970) published a standard that exposure to the general public in uncontrolled areas not be more than 1.4 mR/day (assuming 1.0 mR results in 1.0 millirems of absorbed gamma radiation). However, the Department of Energy (1977) recommended that 170 millirems per year should be the limit for individuals and population groups in uncontrolled areas. This would be equivalent to 0.5 mR/day if an exposure of 0.5 mR/day results in an absorbed dose of 0.5 millirem. The average exposure to small mammals on tailings covered with 30 cm of soil exceeded this limit, even after exposures from the control were subtracted as background. The uranium tailings with 30 cm of shale and 60 cm of topsoil also had exposure rates that slightly exceeded this recommendation. If exposure to animals on the control were subtracted as background, then exposure to small mammals on the site with 30 cm of shale and 60 cm of soil was below the U.S. Department of Energy (1977) recommendation. If the U.S. Department of Health, Education and Welfare published standard were accepted, the soil covering of at least 30 cm of soil adequately reduced gamma exposure rates to below 1.4 mR/day.

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Small Mammal Mycophagy near Woody Debris Accumulations in the Stehekin River Valley, Washington

Abstract

The digestive tracts of 32 small mammals (*Sorex monticolus, Peromyscus maniculatus, Microtus longicaudus,* and *Clethrionomys gapperi*) trapped near woody debris piles were examined for presence and abundance of spores of hypogeous, epigeous and wood-inhabiting fungi. All animals contained fungal spores, usually in abundance high enough to suggest that each animal had recently consumed fungi. Spores of hypogeous fungi were the most abundant, especially those of genera *Alpova* and *Rhizopogon.*

Introduction

Fungi are important in the diet of many small mammals (Dowding 1955, Williams 1959, Whitaker 1962, Williams and Finney 1964, Martell 1981, Martell and Macaulay 1981, Ure and Maser 1982, Gunther *et al.,* 1983, McIntire 1984). Small mammals readily consume fruiting bodies of fungi in feeding trials. Hypogeous (subterranean-fruiting) fungi are most commonly consumed, often being preferred foods (Fogel and Trappe 1978, Trappe and Maser 1978, Maser *et al.,* 1978). Also, there is close co-adaptive dependence of some hypogeous fungi and the mammals that consume them (Talbot 1952, Trappe and Maser 1976). Many of these same studies have shown that epigeous (above-ground-fruiting) and wood-inhabiting fungi and lichens are also eaten by small mammals.

Observations in the Stehekin River Valley, Washington suggested that the fungi which inhabit woody debris accumulations (*e.g.* log jams and piles) are sometimes eaten by small mammals; tooth marks were found on sporocarps of *Coriolus sp.*. Small mammals along the river are concentrated in areas of woody debris accumulation (Mason and Koon 1985). The present study was undertaken to assess the importance of wood-inhabiting fungi in the diet of small mammals in the area.

Methods

This study was a part of the Stehekin Woody Debris Accumulation Project (Mason and Koon 1985) along the lower Stehekin River, within the Lake Chelan National Recreation Area, Washington. In the course of monitoring the activity of small mammals along the river with live traps, a number of animals were trapped dead, particularly from the months December to June. Thirty-two carcasses, including representatives of montane shrew (*Sorex monticolus,* 5 examined), deer mouse (*Peromyscus maniculatus,* 21 examined), long-tailed vole (*Microtus longicaudus,* 5 examined) and Gapper's red-backed vole (*Clethrionomys gapperi,* 1 examined), were frozen and later processed. The contents of the alimentary tracts were macerated with a scalpel in about 5 ml of 10 percent formaldehyde solution. The suspension was allowed to settle for several minutes and drops of the settled debris were examined under 400X. At least three drops of the settled material were examined from each animal. Records were made on the characteristics and the abundance of all fungal spores seen in each animal. Other recognizable food materials were noted.

A list was compiled of the characteristics of spores from 122 species and genera of fungi thought to be common in the Stehikin River Valley. This list included fungi previously collected or suspected to be present in the area as well as fungi that were reported in the diet of small mammals of the Pacific Northwest.

Spore characteristics were stored in a computerized synoptic key which allows character-by-character comparison of the unknown spores with characters of the suspected species. Using this key, the spores were identified to species, genus, or unknown spore-type and put into five groups: (1) known hypogeous fungi, (2) probable hypogeous fungi not definitively identified (those spores that were relatively large and/or thick-walled and were not otherwise assignable), (3) uniquely wood-inhabiting fungi, (4) epigeous

fungi definitely non-wood-inhabiting and their wood-inhabiting relatives, and (5) unknown, non-hypogeous fungi.

Results and Discussion

All animals investigated contained spores. All but three animals had spore-types at an abundance which would suggest that sporocarps had been consumed relatively recently (Table 1). Spores were usually the most conspicuous part of the contents, with the exception of starch grains from plant food and trap bait. In addition, there was often a variety of single spores which might have been residual from previous fungal meals or random "spore rain" on other food. Recent feeding experiments show that, following a meal of fungi, fungal spores are observed in digestive tract and/or feces for up to two weeks after the meal (J.M. Trappe, personal communication).

The largest portion of the fungal diet consists of hypogeous fungi, as has been shown for small mammals in other habitats. Small hyaline spores without hilar appendages almost certainly are from any of four species of *Rhizopogon* or from *Alpova diplophloeus* (Table 1). The spores of the other genera of hypogeous fungi recognized are relatively large and/or thick-walled or have other distinctive characters. A number of spores with thick walls and/or larger size, not otherwise assignable, were often abundant. Further evidence supporting the assignment of most spores to hypogeous fungi, is the relatively low abundance of fungal hyphae which are characteristic of epigeous and wood-inhabiting fungal sporocarps.

A few wood-inhabiting-fungal spores were found in the digestive tracts. Spores were assigned to several wood-inhabiting species (*Coriolus hirsutus, Fomitopsis pinicola, Merulius* sp., *Hormomyces aurantiacus*—the conidial state of a jelly fungus and *Xylosphaera hypoxylon*—conidial state or *Hymenoscyphus* sp.). The five species of wood-inhabiting fungi were not particularly abundant in collections of fungi made in the area during the time of the study. Noticeably absent were spores from the more common species of "polypores" (*Cerrena unicolor,* and *Coriolus versicolor, Funalia hispida, Gloeophyllum sepiarum, Osmoporus odoratus, Schizophyllum commune*) and other

TABLE 1. Contents of alimentary canals of small mammals trapped near woody debris accumulations in the Stehekin River Valley. Numbers of animals examined containing spores classified to spore type and abundance class.

Abundance Class*	5	4	3	2
Spores Types**				
1. *Hypogeous*				
Aldi		2		
Endo			1	2
Gaut				2
Glom		1		2
Hymg				3
Rhiz	4	2	5	5
2. *Unknown Hypogeous*	2	3	2	8
3. *Wood-Inhabiting*				
Cohi				1
Fopi			1	1
Hoau		1	1	1
Meru				1
Xyhy/Hyms		1	1	1
4. *Epigeous*				
Aman				1
Copr		1		
Cort			1	1
Gale				1
Pezi				1
Russ				1
Suil			1	
5. *Unknown Epigeous or Wood*	1	2	9	13

**Abundance classes (at least 10 fields viewed in 3 drops of contents under 400X):*
5—In every field, usually extremely abundant
4—Often seen, but not in every field
3—In 1/2 to 1/4 of fields viewed, or locally concentrated
2—occasional: more than one time in 1/4 of the fields viewed

***Species codes of spore types*
Aldi *Alpova diplophloeus* (Zeller and Dodge) Trappe and Smith
Endo *Endogone* spp.
Gaut *Gautieria* spp.
Glom *Glomus* spp.
Hymg *Hymenogaster* spp.
Rhiz *Rhizopogon parksii* Smith (these four species have spores of the size observed)
Rhiz *R. smithii* Hosford
Rhiz *R. subareolatus* Smith
Rhiz *R. subsalmonius* Smith

Epigeous and Wood-Inhabiting Fungi
Aman *Amanita* spp.
Cohi *Coriolus hirsutus* (Wulf. ex Fr.) Quél
Copr *Coprinus* spp.
Cort *Cortinarius* spp.
Gale *Galerina* spp. or *Crepidotus* spp.
Fopi *Fomitopsis pinicola* (Fr.) Karsten
Hoau *Hormomyces aurantiacus?* (imperfect state of *Tremella* sp.)
Hyms *Hymenoscyphus* spp.
Meru *Merulius* spp.
Pezi *Peziza* spp.
Russ *Russula* spp.
Suil *Suillus* spp. or other "boletes"
Xyhy *Xylosphaera hypoxylon* (L. ex Hooker) Dumortier

fungi (*Hericium ramosum, Pholiota destruens, Pleurotus* spp.) which commonly fruit on woody debris in the area.

Several epigeous genera (*Coprinus, Cortinarius, Galerina, Russula* and *Suillus*) were identified from distinguishable shape, ornamentation, and/or pigmentation of their spores.

Teeth marks were observed on sporocarps of *Coriolus* spp. during field work, particularly in late summer and early fall when sporocarps first mature, and are less "woody" in texture. However only one case of consumption of *Coriolus hirsutus* was confirmed.

Fungi fruit seasonally epigeous and wood-inhabiting fungi occur whenever temperatures are warm enough and there is suitable moisture in their substrates. Sporocarps from wood-inhabiting polypores would be most palatable when first fresh, since they become woodier as they mature. Fresh polypores might not have identifiable spores. Larger, fleshy, wood-inhabiting sporocarps are likely to be more palatable, and are abundant in the area for relatively short periods. In the Stehekin River Valley, the peak of fruiting of these species occurs from May to early June and late August to early November, depending on seasonal weather patterns. Although hypogeous fungi fruit all year long, peak times of fruiting generally occur between November and June (Fogel 1976, 1981). The absence in the digestive tracts of the most common wood-inhabiting species of fungi may be explained in part by the fact that most of the animals examined were trapped during winter and spring months, when such fungi are absent or less common.

Of the four genera of mammals studied, *Clethrionomys* is considered the most selective in its preference for fungi over other types of food, but species in all four genera have been shown to consume fungi in previous studies (Master *et al.* 1978, Fogel and Trappe 1978). The four species of animals observed showed no individual preferences for different types of fungi.

One hypogeous fungus tentatively identified from spores as *Alpova diplophloeus,* shows restricted mycorrhizal host preference for species of alder (*Alnus,* Molina 1981). Since both red alder (*A. rubra*) and Sitka alder (*A. sinuata*) are common locally, it is possible that this fungus is important in small mammal diets in the study area.

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Radionuclide Concentrations in Wildlife Occurring at a Solid Radioactive Waste Disposal Area

Abstract

Of 18 mammalian species observed during a 24-month period at a solid radioactive waste storage and disposal area in southeastern Idaho, deer mice had the highest concentration of radionuclides (^{90}Sr, ^{137}Cs, ^{238}Pu, $^{239,240}Pu$, and ^{241}Am) in tissues. Cottontail rabbit carcass samples from the disposal area had significantly greater concentrations of ^{241}Am than carcass samples from a control area. Background levels of radionuclides were detected in horned lark, mourning dove, and sage grouse. Coyote fecal samples from the disposal area had significantly greater concentrations of ^{241}Am than those from a control area, probably due to their consumption of contaminated small mammals. Results of these studies indicate that the numerous species of wildlife that inhabit the solid radioactive waste disposal area do not contribute significant quantities of radionuclides to the surrounding environment.

Introduction

The world's largest complex of nuclear reactors, a nuclear fuel reprocessing plant, and other associated testing and training facilities are located on the 230,000 ha Idaho National Engineering Laboratory (INEL) in southeastern Idaho. Since 1952, solid waste contaminated with activation and fission radionuclides from these facilities has been disposed below ground at the Radioactive Waste Management Complex (RWMC) of the INEL. In addition, transuranic waste from the U.S. Department of Energy's Rocky Flats facility in Colorado has been disposed or stored at the RWMC since 1954.

Shallow land burial is currently the most common method for disposal of solid low-level radioactive waste in the United States. In order to assess the environmental consequences of such disposal, data are needed to estimate radionuclide transport processes and migration rates. One potential mode of radionuclide transport is through invertebrate and vertebrate species that reside in, or travel through, radioactive waste disposal areas. Radionuclides may be assimilated when these species ingest other animals, vegetation, or soil and through inhalation and attachment of contaminated soil particles to skin, hair, or feathers. Radionuclides could be transported when animals disperse or migrate from the area or through predator-prey food webs (Arthur and Markham 1982a). Also, burrowing animals could excavate contaminated soil to the surface (Arthur and Markham 1983) which could be further transported by wind and water (Markham *et al.* 1978).

The purpose of this paper is to compare radionuclide concentrations in tissues of common vertebrate species. Information obtained from this and other radiological research projects conducted in the RWMC area will be utilized to determine the overall role of wildlife species in radionuclide uptake and transport at the low-level radioactive waste disposal area.

Study Area

The INEL is located in a cool desert shrub biome with warm and dry summers and cold, dry winters. Annual average temperature is 5.6°C with recorded extremes of 39°C and −47°C. Average annual precipitation is 22 cm, the

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majority accumulating in late spring and winter. Geologic features consist of successive subsurface basalt flows and interbedded sediments overlain by 1.0 to 7.6 m (average 5.0 m) of lacustrine and eolian deposits. Soil materials are unconsolidated clay, silt, and gravel.

The RWMC (elevation 1527 m) occupies 55 ha of the INEL and consists of two areas, the Transuranic Storage Area (TSA) and Subsurface Disposal Area (SDA). TSA is 19 ha in area; 8 ha was utilized for interim storage of transuranic wastes. The eastern portion contains some undisturbed big sagebrush (*Artemisia tridentata*) vegetation. A part of the SDA (36 ha in total area) has been seeded with crested wheatgrass (*Agropyron cristatum*); areas not seeded were invaded by Russian thistle (*Salsola kali*) and summer cypress (*Kochia scoparia*). Undisturbed areas peripheral to the RWMC are dominated by big sagebrush, bluebunch wheatgrass (*Agropyron spicatum*), and green rabbitbrush (*Chrysothamnus viscidiflorus*) (McBride *et al.* 1978).

Rodent species inhabiting the RWMC include 11 small mammal species (Groves 1981) of which the deer mouse (*Peromyscus maniculatus*), Ord's kangaroo rat (*Dipodomys ordii*), and montane vole (*Microtus montanus*) are the most common. Pygmy rabbit (*Sylvilagus idahoensis*), Nuttall's cottontail rabbit (*Sylvilagus nuttallii*), black-tailed jackrabbits (*Lepus californicus*), and horned lark (*Eremophila alpestris*) also occur at the RWMC. Commonly occurring game species include mule deer (*Odocoileus hemionus*), pronghorn (*Antilocapra americana*), sage grouse (*Centocercus urophasianus*) and mourning dove (*Zenaida macroura*). The most common predators in the area include the long-tailed weasel (*Mustela frenata*), coyote (*Canis latrans*), rough-legged hawk (*Buteo lagopus*), golden eagle (*Aquila chrysaetos*), and the great horned owl (*Bubo virginianus*).

TSA storage consists of metal drums or fiberglass-coated wooden boxes stacked aboveground on an asphalt pad. Plywood, plastic, and at least 0.9 m of soil covers the waste when pad areas become full. In SDA, wastes packaged in boxes, plastic-wrapped parcels, or uncontained are disposed by shallow-land burial practices. A greater potential for radionuclide migration is inherent in SDA disposal compared with storage at TSA because of different operational methods, use of different containers, and the duration of waste confinement. Therefore, in this paper, emphasis is given to radionuclide migration from the SDA disposal area rather than from other areas at the RWMC.

A wide variety of activation, fission, and transuranic wastes have been disposed in the SDA. Low-level activation and fission wastes are disposed in trenches which average 275 m long by 3 m wide, and approximately 4 m deep. These wastes consist of laboratory equipment, filters, paper, protective clothing, and building materials. Larger, irregular shaped material (pipes, empty liquid tanks, and other noncompactible items) are disposed in pits which average 30 m wide and 4 m deep, and vary in length. Transuranic waste disposed prior to 1971 was enclosed in steel drums or cardboard cartons; wooden crates were used for large items. Most transuranic waste was buried in pits, although some earlier shipments were interspersed in trenches with activation and fission waste. After pits and trenches are filled with waste, at least 0.6 m of soil is applied and compacted over the surface as a final cover.

Approximately 8.6 x 10^6 Ci of radioactive wastes have been disposed in the SDA since 1952. The current quantity of activity remaining in disposed waste is greatly reduced due to radioactive decay. No estimate is available of the quantity of specific radionuclides placed in the SDA prior to 1971; however, during the 1971-78 period 392 800 Ci of ^{60}Co, 4 104 Ci of ^{90}Sr, and 4 700 Ci of ^{137}Cs had been disposed in the SDA. Short-lived radionuclides frequently disposed include ^{51}Cr, ^{54}Mn, ^{58}Co, ^{59}Fe, ^{95}Zr, ^{103}Ru, ^{141}Ce, and ^{144}Ce. The major transuranic nuclides and the quantities placed in the SDA are ^{238}Pu (571 Ci), ^{239}Pu (21 050 Ci), ^{240}Pu (4 935 Ci), ^{241}Pu (179 000 Ci), and ^{241}Am (48 010 Ci).

Methods

Tissues from common wildlife species were sampled as part of other ecological studies at the RWMC (Arthur and Markham 1978) and analyzed for radionuclide concentrations. Deer mice, collected with museum special snap traps, were sampled for hide and carcass tissues; due to their small masses, tissues of at least four mice were composited for analyses. Hide and carcass tissues were sampled from cottontail rabbits (Janke and Arthur 1985). Muscle tissues of sage grouse

(Connelly and Markham 1982) and mourning dove (Markham and Halford 1982) were sampled and analyzed for radionuclide concentrations, whereas horned larks were analyzed whole. Coyote fecal samples were collected in and immediately adjacent to the SDA to estimate the quantity of radioactivity transported by a predatory species (Arthur and Markham 1982a). Tissue samples were also collected from wildlife species in control areas located at least 60 km from the SDA (off INEL), to assess radionuclide concentrations in wildlife not associated with radioactive waste disposal.

After dissection, all tissues were weighed (wet weight) and analyzed for gamma-emitting radionuclides on a 65 cm germanium-lithium detector coupled to a computerized multichannel analyzer system. Deer mice, rabbit tissues, and coyote fecal samples were dried for 72 hours at 80°C, weighed, and sent to a commercial laboratory for ^{90}Sr, ^{238}Pu, ^{239,240}Pu, and ^{241}Am analysis (Wessman *et al.* 1971). Lowest detectable concentrations (pCi/g wet weight) for commonly detected radionuclides were 0.09 for ^{90}Sr, 0.2 for ^{137}Cs, and 0.004 for ^{238}Pu, ^{239,240}Pu, and ^{241}Am.

A Student's t-test was used to determine whether radionuclide concentrations were significantly different between the SDA and control samples. A significance level of $P \leq 0.05$ was used for rejection of null hypotheses. Although ^{7}Be, ^{40}K, ^{208}Tl, ^{212}Pb, ^{214}Pb, and ^{214}Bi were frequently detected in tissue samples, no statistical analyses were performed on those radionuclides due to their natural occurrence in the environment.

Results

Deer mouse tissues had the highest radionuclide concentrations of the wildlife species collected at the SDA. Above background concentrations of ^{137}Cs, ^{238}Pu, ^{239,240}Pu, and ^{241}Am were detected in hide samples, whereas the highest mean concentration of ^{90}Sr was detected in carcass tissues (Table 1). Elevated ^{90}Sr concentrations in carcass samples indicated that ingestion, and subsequent tissue assimilation, was a more important uptake mechanism than hide contamination.

Radionuclide concentrations in SDA cottontail rabbit tissues were not significantly ($P > 0.05$) greater than control area values with one exception. Americium-241 (0.01 pCi/g) in carcass samples was significantly greater than in control rabbit carcasses (0.001 pCi/g). The ^{241}Am concentrations in rabbit carcasses were similar to those detected in deer mouse carcasses. Fission nuclides (other than ^{90}Sr and ^{137}Cs) occurring in rabbit tissues included ^{51}Cr, ^{54}Mn, ^{60}Co, ^{134}Cs, and ^{140}Ba, each occurring in one SDA sample.

Horned lark, sage grouse, and mourning dove tissue samples from the SDA and control areas were analyzed for gamma-emitting radionuclides. No significant ($P > 0.05$) difference was observed between ^{137}Cs concentrations in 10 SDA (1.07 ± 2.51 pCi/g) and five control (0.21 ± 0.16 pCi/g) horned lark samples. Other fission products detected in horned larks were ^{60}Co and ^{137}Te, each detected in one sample. Comparisons between sage grouse muscle samples indicated no significant difference in ^{137}Cs concentration between the SDA and control population (Connelly and Markham 1982). Similarly, no significant difference was observed for ^{137}Cs concentrations in muscle samples of mourning dove (Markham and Halford 1982).

No coyote tissue samples were collected; however, 24 SDA and 12 control fecal samples were analyzed for radionuclides. No significant differences were observed between SDA and control area coyote fecal concentrations for ^{90}Sr, ^{137}Cs, ^{238}Pu, and ^{239,240}Pu; however ^{241}Am concentrations in SDA coyote feces (0.41 pCi/g) were significantly ($P < 0.05$) greater than control feces concentrations (0.008 pCi/g) (Arthur and Markham 1982a). Americium levels in SDA coyote feces were similar to levels detected in SDA deer mice tissues, indicating that ingestion of the small mammals was likely the source of americium in coyote feces.

Few samples were obtained from other SDA wildlife species. Cesium-137 concentrations ($\bar{x} = 0.32$ pCi/g) in three rattlesnake (*Crotalus viridis*) carcass samples were at background levels; no other gamma-emitting nuclides were detected. Comparisons between three composite samples of invertebrates from the SDA, and one control area sample, indicated low radionuclide concentrations. Radionuclide concentrations detected in SDA invertebrate samples were 2.4 pCi/g ^{90}Sr, 0.47 pCi/g ^{137}Cs, 0.008 pCi/g ^{238}Pu, 0.078 pCi/g ^{239,240}Pu, and 0.022 ^{241}Am. No transuranics were detected in control samples; ^{90}Sr and ^{137}Cs concentrations averaged 0.7 and 3.7 pCi/g, respectively.

TABLE 1. Radionuclide concentration (pCi/g) in wildlife collected in and adjacent to the Subsurface Disposal Area and at control areas in southeastern Idaho.

Species	Tissue	Area	Sample Size	Mean Radionuclide Concentration ($\bar{x}$ + SD pCi/g)				
				^{90}Sr	^{137}Cs	^{238}Pu	$^{239,240}Pu$	^{241}Am
Coyote[1]	Feces	SDA	24	2.0 ± 1.6	3.4 ± 6.5	0.013 ± 0.027	0.5 ± 1.2	0.4* ± 0.9
		Control	12	0.9 ± 0.2	0.7 ± 0.5	0.003 ± 0.004	0.006 ± 0.003	0.003 ± 0.002
Horned Lark	Carcass	SDA	9	---[6]	1.07 ± 2.51	---	---	---
		Control	5	---	0.21 ± 0.16	---	---	---
Great Basin Rattlesnake	Carcass	SDA	3	---	0.32 ± 0.21	---	---	---
		Control	0					
Invertebrates	Composites	SDA	3	2.4 ± 3.2	0.47 ± 0.55	0.008 ± 0.011	0.078 ± 0.11	0.022 ± 0.020
		Control	1	0.7	3.7	BDL	BDL	BDL
Deer Mice[2]	Carcass	SDA	21	721* ± 1061	57.3* ± 122	0.01 ± 0.03	0.04 ± 0.11	0.01 ± 0.02
		Control	5	0.6 ± 0.6	0.20 ± 0.07	0.002 ± 0.003	0.002 ± 0.007	0.003 ± 0.002
	Hide	SDA	21	417* ± 612	78.5 ± 132	0.54* ± 1.96	0.36* ± 0.66	0.27 ± 0.83
		Control	5	1.3 ± 0.9	2.4 ± 0.5	0.002 ± 0.002	0.007 ± 0.006	0.039 ± 0.050
Sage Grouse[3]	Muscle	SDA	14	---	0.3 ± 0.09			
		Control	20	---	0.3 ± 0.2			
Nuttall's[4]	Carcass	SDA	10	0.30 ± 0.24	0.14 ± 0.33	0.001 ± 0.0004	0.004 ± 0.003	0.010* ± 0.009
		Control	5	0.37 ± 0.09	0.16 ± 0.12	0.001 ± 0.001	0.002 ± 0.001	0.001 ± 0.001
	Hide	SDA	10	0.45 ± 0.18	0.18 ± 0.15	0.002 ± 0.002	0.009 ± 0.010	0.029 ± 0.046
		Control	5	0.44 ± 0.15	0.31 ± 0.07	0.004 ± 0.003	0.002 ± 0.001	0.002 ± 0.001
Mourning[5] Dove	Muscle	SDA	12	---	0.63	---	---	---
		Control	11	---	0.75	---	---	---

[1]Arthur and Markham 1982a [2]Arthur *et al.* 1983 [3]Connelly and Markham 1982 [4]Janke and Arthur 1984 [5]Markham and Halford 1982

[6]Sample not analyzed for this radionuclide.

*Significant difference ($P \leq 0.05$) between SDA and control area concentration for this radionuclide.

Discussion

Data from this study provided information on the relative importance of certain vertebrates in radionuclide transport in the environment surrounding a low-level radioactive waste disposal area in southeastern Idaho. Due to their large biomass, small mammal species at the SDA such as deer mouse, Ord's kangaroo rat, montane vole, and Townsend's ground squirrel had the greatest potential for radionuclide assimilation and transport. Ingestion and hide contamination appeared to be the most important sources of elevated radionuclide concentrations.

Deer mouse tissues had the highest mean radionuclide concentrations of the wildlife species sampled at the SDA. Recent research indicated that an annual total of 22.8 μCi (^{90}Sr, ^{137}Cs, ^{238}Pu, ^{239,240}Pu, and ^{241}Am) occurred in the deer mouse population inhabiting the SDA (Arthur *et al.* In press), as compared to 0.1 μCi occurring in a deer mouse population of equal size at a control area. Population estimates were based on a minimum of 6160 deer mice inhabiting the waste disposal area over a 1-year period. Of that 22.8 μCi activity, 22.7 μCi was due to the nuclides ^{90}Sr and ^{137}Cs.

Because deer mice were estimated to comprise 31 percent (106 of 346 kg live-weight) of the SDA total rodent biomass (Groves and Keller 1983), the estimate of 22.8 μCi transported by deer mice is only a portion of the total radioactivity in the SDA rodent population. By assuming that the other nine rodent species trapped in the SDA had tissue radionuclide concentrations similar to deer mice, a total of 73.5 μCi would occur in the SDA rodent population (Arthur and Markham 1982b). Even though the inventory for SDA rodents is higher than that for the control area, the overall quantity of radioactivity transported by these species is small.

In addition to rodent species, cottontail rabbits also commonly inhabit the SDA. Although a greater concentration of ^{241}Am occurred in carcass tissues of cottontails inhabiting the SDA, the total activity of radionuclides in the rabbit population at the SDA (11.2 nCi) was not significantly different from that estimated for control rabbits (13.2 nCi) (Janke and Arthur 1985).

The low use of the SDA by avian species is likely due to human intervention and because the SDA was dominated by crested wheatgrass, a vegetation type which has been shown to support fewer nesting species and fewer individual birds than sagebrush areas at the INEL (Reynolds 1978). Of the 31 bird species identified, tissues were collected from three common species. Neither horned lark, mourning dove, nor sage grouse tissues had significantly greater ^{137}Cs concentrations than control area values for these species.

An annual total of 7.2 μCi (^{90}Sr, ^{137}Cs, ^{238}Pu, ^{239,240}Pu, and ^{241}Am) was present in feces eliminated by coyotes within a 6.3 km radius of the SDA, compared to a total of 1.8 μCi in feces eliminated by an equal number of coyotes in a control area (Arthur and Markham 1982a). Due to their limited use of the RWMC and the low quantity of radionuclides excreted by coyotes, it is doubtful that any environmental consequences occur as a result of this transport vector.

Previous studies have concluded that wildlife species can be modes of radionuclide transport in ecosystems having radioactive contamination (O'Farrell and Gilbert 1975, Halford *et al.* 1981). Some wildlife species inhabiting the SDA had contacted areas of radioactive contamination and assimilated above-background levels of radionuclides in tissues. This was particularly true for species such as small mammals which burrow into areas of disposed waste and subsurface soil contamination (Arthur and Markham 1983). Larger mammals and bird species had radionuclide levels similar to that in control samples. Transport of radionuclides by coyotes occurs but is minimal. Only for cottontail rabbits, small mammals, and coyotes were estimates available on the quantity of radioactivity contained in tissues and/or exported. For these species a total of 80.7 μCi (^{90}Sr, ^{137}Cs, ^{238}Pu, ^{239,240}Pu, and ^{241}Am) was contained in tissues or feces over a one year period.

More important than the occurrence of radionuclides in animal tissues or feces, may be the effect of these species on soil covers over disposed waste. Recent research concluded that over a one year period, small mammal soil excavations brought 11 700 kg soil containing 45 μCi radioactivity to the SDA surface (Arthur and Markham 1983). Additionally, burrowing may increase moisture infiltration rates into soil. Studies currently being conducted at the INEL will determine the impact of biotic intrusion on soils cover-

ing disposed radio-active waste and utilize this information to recommend stabilization techniques for shallow-land radioactive waste disposal.

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Petrographic Differences Between Two Sedimentary Rock Bodies of the Eocene-Age Manastash Formation, Kittitas County, Washington

Abstract

Regression analysis of grain size on quartz and feldspar content of 27 sandstone samples from two adjacent sedimentary rock bodies of the Manastash Formation show that as grain size increases, quartz content increases, and as grain size decreases, feldspar content increases. T-tests, comparing the slopes and intercepts of similar regression equations for quartz versus grain-size and for feldspar versus grain-size of the rock bodies, indicate compositional variations unrelated to grain-size differences. Mineralogical variations are probably caused by petrographic differences in the source rock related to uplift and erosion that exposed rocks of differing composition.

Introduction

Although sedimentary rocks are fairly widespread along the flanks of the north and central Cascade Mountains of Washington, the lateral relationships between geographically separate deposits are not well understood. Correlations are difficult to establish, because of a lack of either prominent marker beds or obvious guide fossils within these lithologically similar units. The sedimentary rocks are predominantly composed of arkosic sandstones which are 18-48 percent feldspar (mostly plagioclase) and 40-78 percent quartz (Frizzell 1979). Plant fossil remains in intercalated shales suggest that most of the sedimentary rock bodies are Eocene to Paleocene (?) in age (Newman 1981). Radiometric dates of volcanic rocks interbedded with the sedimentary rocks are generally Eocene in age, but the results vary widely due to alteration of the volcanic material after deposition (Frizzell 1979, Tabor *et al.* 1984).

Recent studies have shown that the mineral composition of sand changes with grain size and that this relationship may be useful in solving problems in the Manastash Formation concerning the source rocks, climate, depositional environment, or age relationships between sedimentary rock bodies (Flores 1967, Davis and Ehrlich 1974, Basu 1976). This study utilizes similar methods in order to resolve a problem of origin and age relationships of two separate, but proximal, bodies of Tertiary sedimentary rocks in central Washington.

The study area is located about 8 km south of Cle Elum, Washington, where 1.6 to 3 km of younger volcanic flows, tuffs, and volcaniclastic rocks separate two sedimentary rock bodies of the Eocene-age Manastash Formation (see areas A and B on Figure 1). Sedimentary rocks in area A have a thickness of approximately 1,000 m, while the rocks in area B have a maximum thickness of 750 m. Both areas unconformably overlie crystalline rocks composed of schist, phyllite, and quartz-diorite gneiss (Stout 1962), and both are unconformably overlain by Eocene-age volcanic flows, tuffs, and volcaniclastic rocks. Both rock bodies are composed mostly of arkosic sandstone with minor amounts of shale, siltstone, conglomerate, and coal. However, area B rocks are substantially coarser grained and more quartzose than area A rocks, which are comparatively feldspar-rich. Previous studies indicate that these rocks were deposited by fluvial processes (Lewellen 1983) within a warm, temperate to subtropical climate (Stout 1957), and that area B rocks may be older than area A rocks (Newman 1981).

Differences in the trends of grain size versus mineral composition of the sedimentary rocks of area A and B were analyzed in an effort to resolve the problems of depositional and age relationships. The presently disjunct bodies may be remnants of a once larger sedimentary unit, if differences in mineral contents are a reflection of differing grain sizes caused by depositional processes. Conversely, mineralogical differences greater than those associated with grain-size variations may indicate that the sandstones represent different ages, source areas, or other unrelated depositional factors.

Methods

Fourteen sandstone samples from area A and thirteen from area B were collected at sites that reflect the areal and stratigraphic variations in the two rock bodies (Figure 1). Thin sections were prepared and stained for potassium feldspar and plagioclase according to the techniques of Lainz *et al.* (1964) and Norman (1974). The approximate grain size of each sample was expressed accord-

Figure 1. Location map of the study area and the sandstone samples.

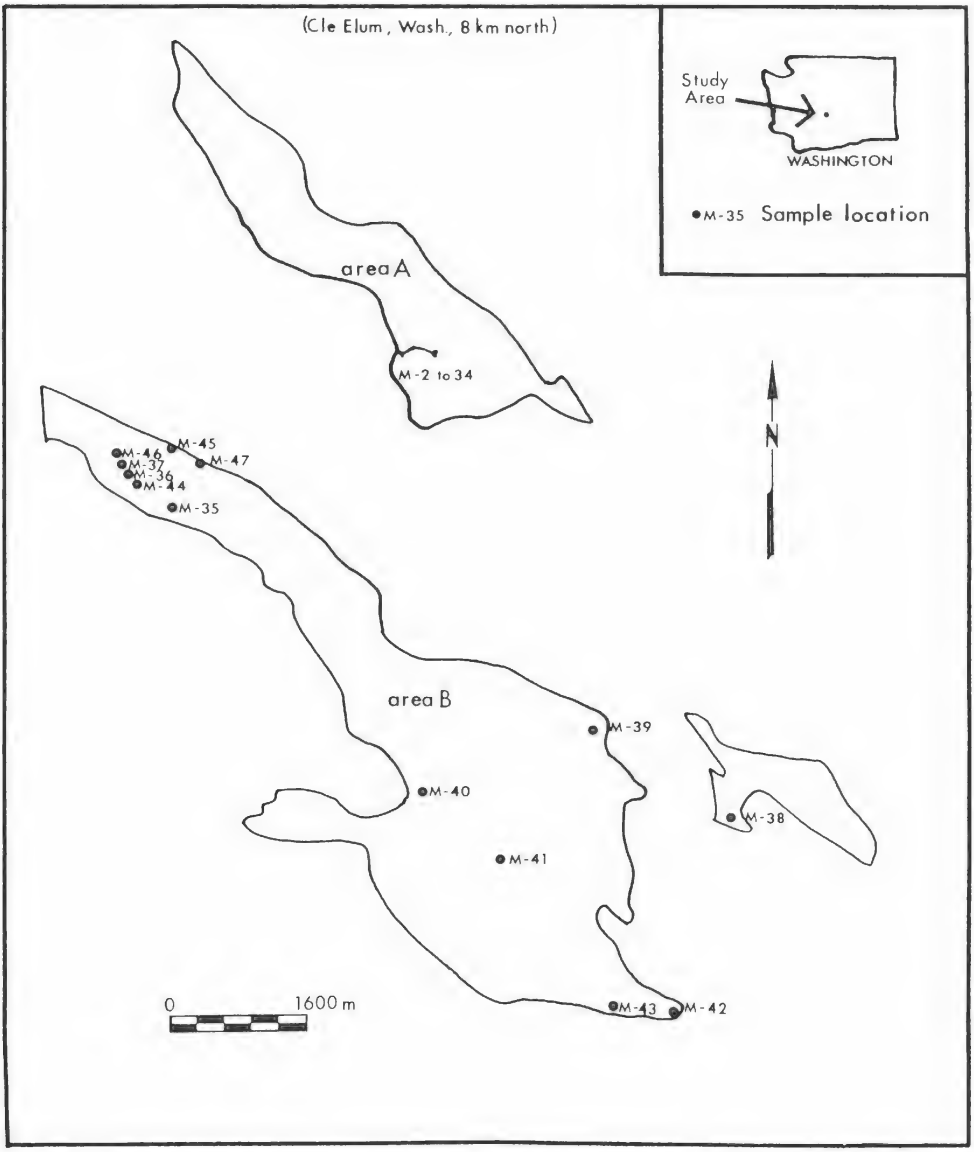

TABLE 1 .Grain size and relative percent quantities of quartz and feldspar measured in each sample.

Location	Quartz	Feldspar	Grain Size
m-2	49	51	very fine
m-4	39	61	very fine
m-6	36	64	fine
m-8	22	78	very fine
m-10	31	69	fine
m-13	49	51	course
m-14	43	57	fine to medium
m-16	46	54	fine
m-17	38	62	very fine
m-23	39	61	very fine
m-27	35	65	very fine
m-29	43	57	fine
m-33	37	63	very fine
m-34	52	48	medium
m-35	91	9	coarse
m-36	88	12	coarse
m-37	67	33	fine
m-38	82	18	coarse
m-39	78	22	medium
m-40	87	13	coarse
m-41	93	7	coarse
m-42	69	31	coarse
m-43	67	33	medium to coarse
m-44	80	20	coarse
m-45	59	41	fine to medium
m-46	80	20	medium to coarse
m-47	68	32	coarse

ing to the Wentworth scale (very-fine, fine, medium, or coarse-grained sandstone) based on average measurement of the long axis of 10 to 15 feldspar or quartz grains randomly selected through the use of a random digit table. Detrital components were determined by point counting an average of 800 points per sample (Chayes 1949). Categories of recognized detritus were monocrystalline quartz, polycrystalline quartz, plagioclase, potassium feldspar, volcanic lithics, sedimentary lithics, metamorphic lithics, microgranular lithics, micas, clay-sized material, and a miscellaneous category for those grains that did not fit into any of the other categories.

In order to determine the grain size and mineral composition relationship of the sandstones within each area, linear-regression equations were derived for grain size versus feldspar and quartz contents.

T-tests were used to compare the slopes and intercepts of similar regression equations of the different rock bodies so that mineral composition variations not attributable to grain size changes could be ascertained. Nonsignificant t-test results, determined at a 95 percent confidence level, for the comparison of the slope and intercepts of the linear regression equations from the rock bodies indicate that differences in mineral content are attributable to grain-size trends. Significant t-test results for the slope, intercept, or both indicate differences greater than those associated with grain size variations and require other explanations.

Results and Discussion

The mineral composition and the grain-size measurements for each sample are given in Table 1. In general, sandstone samples are very-fine grained in area A and coarse grained in area B. The average composition of the samples in area A is 40 percent quartz, 58 percent feldspar, and 3 percent rock fragments, whereas area B samples average 67 percent quartz, 20 percent feldspar, and 13 percent rock fragments. These sets of averages are very similar to those of the sandstone units derived from uplifted blocks of Holocene to Precambrian age granitic rocks studied by Dickinson and Suczek (1979).

Figure 2 gives the linear-regression data of grain size on quartz and feldspar content for each area. These data indicate that as grain size decreases, feldspar content increases, and quartz content decreases. T-tests indicate that the slopes of like regression equations from each area are not significantly different. However, t-tests of the intercepts of similar regression equations are significantly different. Although some of the variations in mineral composition are attributable to grain size, additional compositional differences not related to grain size exist between the rocks of areas A and B (Table 2).

TABLE 2. Results of t-tests of the slope (b) and the intercepts (a) of the regression equations from areas A and B.

Hypothesis	T-test[a]
$H_o: b_A = b_B$ $H_1: b_A \neq b_B$	$t = 0.877^b$ df = 23
$H_o: a_A = a_B$ $H_1: a_A \neq a_B$	$t = 3.021^c$ df = 23

a $\alpha = .05$, $t = 2.069$
b differences are nonsignificant
c differences are significant

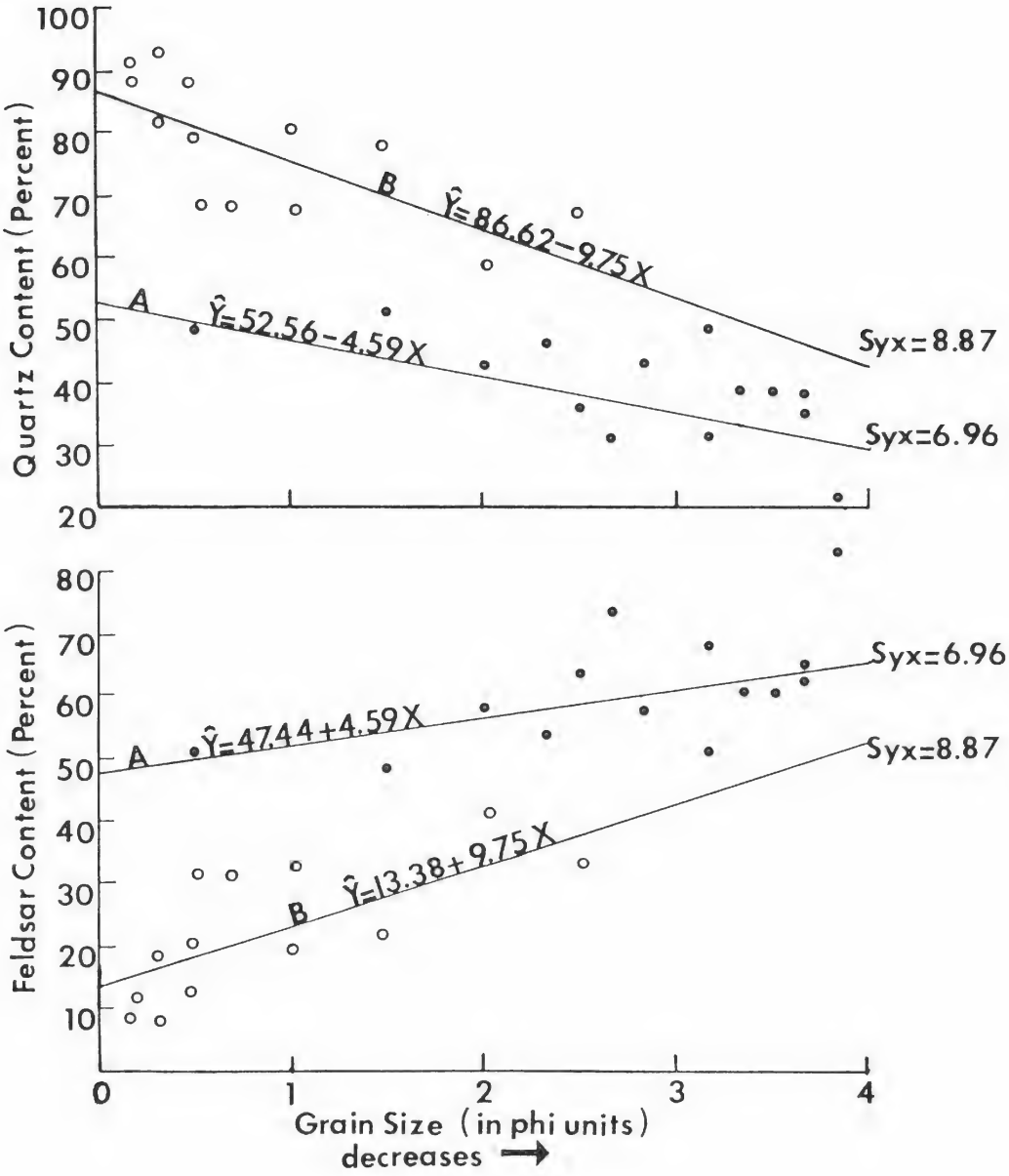

Figure 2. Scatter plot of grain size versus quartz and feldspar content of 27 samples from area A (solid circles) and area B (open circles).

The data indicate that the rocks of areas A and B probably represent two separate depositional events, probably of differing ages. Such a conclusion is consistent with the fossil plant evidence of Newman (1981).

Disregarding grain-size trends, the higher quartz contents of area B sandstone may reflect climatically induced differences in the degree of weathering and soil formation processes in the source rocks. For example, sand samples collected in modern streams draining granitic rocks, not more than 19 km from the source rock, in the warm moist climate of the southern Appalachians, contain less feldspar and more quartz for a given grain size than those from the cool dry northern Rocky Mountains (Basu 1976). Linear-regression equations for the Appalachian data are similar to those of area B, whereas equations for the modern Rocky Mountain data are nearly identical to those of area A (Table 3).

TABLE 3. Comparison of linear-regression equations from this study and from Basu's (1976) study.

Source	Quartz Content Regressed on Grain Size	Feldspar Content Regressed on Grain Size
Appalachians	$\hat{Y} = 77.83 - 6.33x$	$\hat{Y} = 22.17 + 6.33x$
Basu (1976) Area B	$\hat{Y} = 86.62 - 9.75x$	$\hat{Y} = 13.38 + 9.75x$
Rockies	$\hat{Y} = 48.17 - 3.67x$	$\hat{Y} = 51.83 + 3.67X$
Basu (1976) Area A	$\hat{Y} = 52.56 - 4.59x$	$\hat{Y} = 47.44 + 4.59x$

Paleobotanical data from the Manastash rocks indicate a warm, wet climate at the site of deposition, thus the observed compositional differences between areas A and B could reflect climatic differences in the source terranes, particularly if an age difference exists between the two areas. Considering the short distances between the sediment source and the site of deposition, however, the *chances* of radically different climates seem remote. Basu's sediments were collected within 19 km of their source and the likelihood of rapid climatic changes within 19 km in the Manastash source region appears to be small.

A more likely explanation is that compositional differences in quartz and feldspar content reflect different source rocks. Suitable source terranes include a wide variety of crystalline rocks extending from central Washington to central Idaho. Although most of these rocks are granitic or gneissic, which would yield sediments similar to the composition of the rocks in area A, others are low- to medium-grade metamorphic rocks cut by numerous quartz veins. These quartz-rich rocks could presumably provide substantial quartz detritus, and the accompanying micaceous minerals of the metamorphic rocks could be broken down during transport and carried beyond the area of deposition as fine-silt and clay particles. A mixed source terrane of granitic and low- to medium-grade metamorphic rocks could provide the detritus represented in the Manastash Formation by the rocks of area B, which are nearly 70 percent quartz.

Different source rocks most likely account for the mineralogical differences between the rocks of areas A and B. As such the detritus was either derived from two geographically separate source terranes or from erosion of the same site through time. In the latter case, the older rocks of area B were derived from low- to medium-grade, quartz-rich metamorphic rocks, whereas area A received detritus from an underlying intrusive granitic pluton or gneiss exposed after erosion of the overlying rocks.

Conclusions

Analysis of mineral composition and grain size of two geographically adjacent bodies of early Tertiary arkosic sedimentary rocks separated by younger volcanic rocks in central Washington indicate that the two rock bodies are mineralogically distinct after grain size effects are taken into account. The rock bodies are therefore inferred to be of different ages; a conclusion that is in accord with previously reported paleobotanical findings. Differences in mineral composition of the two bodies can be attributed to differences in climate or petrographic characteristics of the source terrane from which the sediments were derived. However, the most likely explanation is that petrographic differences in the source rock are related to an unroofing sequence caused by

uplift and erosion that exposed rocks of differing compositon.

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Conifer Invasion of Subalpine Meadows, Central Lemhi Mountains, Idaho

Abstract

Ages of invasive trees in three subalpine meadows were determined with an increment borer. Climate change, forest fire history, and grazing pressures have all influenced the histories of meadow invasion. Invasive limber pine (*Pinus flexilis*) gave way to Douglas-fir (*Pseudotsuga menziesii*) and lodgepole pine (*Pinus contorta*) during the period of major climate-caused invasion around 1895-1915. Invasions into the meadows in 1920-1940 were a result of drier climatic conditions, the possible influence of grazing, and a forest fire. Heavy grazing prevents present-day invasion in at least one meadow.

Introduction

The determination of periods of climate change, and knowledge about the geographic extent of such changes, provide the basis for an increased understanding of the potential impact of future climatic fluctuations. Unfortunately, many areas in the American west suffer from a paucity of widespread, long-term climatic data which could document such changes. Surrogate data become significant in such locations.

In the mountains of the western United States, subalpine forest environments are difficult sites for tree establishment (Agee and Smith 1984). When trees do become established in locations such as above present treeline or in subalpine meadows, the establishment is often attributed to some form of climate change which has made conditions more amenable for tree survival (Franklin *et al.* 1971, Schimpf *et al.* 1980, Kearney 1982, Ostler *et al.* 1982, Winter 1984). Other factors, particularly land-use practices, must also be examined as possible causative factors in successful tree establishment at formerly inhospitable sites (Dunwiddie 1977, Vale 1981b).

A recent study from the Lemhi Mountains of east-central Idaho (Figure 1) revealed a major historic treeline advance, initiated in the 1920s (Winter 1984). This advance was correlated with a broad climatic warming and drying that occurred across western North America during the same period, and which has also been identified by examination of the ages of invasive trees in subalpine meadows (*e.g.,* Franklin *et al.* 1971, Nisle 1981, Agee and Smith 1984). Other studies in western mountain meadows have also identified successful tree establishment in the same period, but did not directly attribute these tree invasions to climate change (Koterba and Habeck 1971, Vale 1981a).

The present study was concerned with 1) identifying the period(s) of successful tree invasion into mountain meadows in the central Lemhi

Figure 1. Location of the study area in east-central Idaho. A and B are the locations of Winter's (1984) upper treeline study sites in the Lemhi Mountains.

Mountains of Idaho, 2) comparing the period(s) of meadow invasion to the period of treeline advance in the same range, identified by Winter (1984), and 3) attempting to identify causal factors which allowed the meadow invasions to occur.

The Study Area

Geology and Geomorphology

The Lemhi Mountains rise abruptly from the northern edge of the Snake River Plain, and extend approximately 160 km in a northwesterly direction. The range crest has a mean altitude of 3,050 m (Knoll 1977). The mountains are composed of highly deformed Paleozoic sedimentary rocks and quartzites, with a few granitic and dioritic intrusives exposed.

The Lemhis are incised by a system of glacially-scoured valleys which are oriented roughly perpendicular (*i.e.*, southwest-northeast) to the crest of the range. Glacial recession and deposition during the late Pleistocene and Holocene have produced complex patterns of moraine and kettle topography in many valleys (Knoll 1977; Butler 1984a,b,c; Butler *et al.* 1983, 1984). Tree-ring studies illustrate that the last stage of the Neoglacial terminated later than in the southern Rockies, in the 1905-1910 period (Knoll 1977, Butler 1983).

Soils

Soils in the valleys are generally thin and stony. Many Holocene glacial/boulder deposits have soil profiles with poorly developed O/A/C horizons. B-horizon development is restricted to soils forming on Pinedale-aged (and older) glacial moraines, or in subalpine meadows (Butler 1984c).

Climate

No climatic data exist for the valleys of the eastern Lemhi Mountains. It is estimated, however, that the eastern front of the range receives about 40-45 cm of precipitation annually. Precipitation at higher elevations may total as much as 75 cm, much of that in the form of snow (Gallup 1962). Modern-day mean annual temperature along the front of the mountains is estimated at 4-6°C. Periods of above-average precipitation in the state of Idaho as a whole were recorded in 1892-1897, 1905-1915, 1940-1950, and 1968-1972. Periods of low rainfall were 1886-1890, 1899-1905, 1920-1940, and 1950-1965 (Nisle 1981).

Vegetation

Douglas-fir (*Pseudotsuga menziesii*) and ponderosa pine (*Pinus ponderosa*) occupy the lower two-thirds of most valleys. These species give way to subalpine fir (*Abies lasiocarpa*), Engelmann spruce (*Picea engelmannii*), limber pine (*Pinus flexilis*), and whitebark pine (*Pinus albicaulis*) at higher elevations. Lodgepole pine (*Pinus contorta*) is a major successional species at low to middle elevations. Upper treeline elevation ranges from about 2,800 to 3,100 m (Winter 1984).

Specific Study Sites

In several of the glaciated valleys of the east-central Lemhi Mountains, subalpine meadows are located along the central axes of the valleys, in positions immediately upvalley of arcuate mid- and late-Pinedale readvance moraines. The meadows are comprised of varying thicknesses of fine-grained sediments which were impounded by the damming action of the moraines. These sediments in some cases record complex environmental fluctuations which accompanied deglaciation and post-glacial recovery (Butler 1984b, 1985; Butler *et al.* 1984). The thickness of the dammed sediments is a function of the proficiency with which the arcuate meadows acted as dams.

Meadow Selection

Three subalpine meadows in the central portion of the Lemhi Mountains, First, Harry's, and Deer Creek, were chosen for this study. The three meadows are located roughly half-way between the two sites examined in Winter's (1984) treeline study (Figure 1), offering a basis of comparison of periods of meadow invasion vs. treeline advance. They have been spared logging of larger trees; other meadows in the south-central portion of the range near Winter's southern study site were heavily logged. Each meadow possesses similar elevations, orientations, and terrain characteristics (Table 1), and each is within or adjacent to valleys for which records of late Neo-

glacial climatic fluctuations are available (Butler 1983, 1984a). Grazing records, necessary for evaluating grazing effects as a possible causal agent of meadow invasion, were available for the valleys in which the meadows are located.

Location, Soils, and Vegetation

First Meadow (FM) and Harry's Meadow (HM) are located in the Mountain Boy Valley. Butler *et al.* (1983, 1984) mapped and described them. Deer Creek Meadow (DCM) is located in Deer Creek Valley, about 2 1/2 km to the northwest. Soils in the meadows (sampled by backhoe- and hand-trenching) are relatively similar (Table 1), in spite of the varying thicknesses of the fine-grained impounded parent material.

Vegetation surrounding the meadows is largely mature Douglas-fir forest. Several isolated limber pine are scattered along the crest of the moraine which dams FM, and some dead limber pine snags are in close proximity to the living specimens. The meadows themselves are conspicuous on aerial-photos and the ground, because of the general absence of mature, large trees. Vegetation in the meadows is primarily sheep fescue (*Festuca ovina*) or Idaho fescue (*F. idahoensis*), with very little bluebunch wheatgrass (*Agropyron spicatum*). Bluegrass (*Poa secunda*) is a secondary species (U.S. Forest Service 1964). Sagebrush (*Artemisia* spp.) is found in all three meadows (Figure 2). Various members of the aster family (Compositae) are found in all three meadows.

Figure 2. Invasive conifers in First Meadow. The arrow points to a portion of the moraine which dammed the sediments comprising the meadow. Sagebrush and grasses dominate the understory vegetation in the foreground.

Grazing History

Grazing records on file in the U.S. Forest Service office in Leadore, Idaho, indicate that all three meadows were grazed by cattle and horses during an unspecified "early part" of the 20th century. Winter (1984) stated that grazing began in 1919 on an allotment immediately to the north of, and more accessible than, the present study area. It is reasonable to assume, then, that grazing did not begin in the meadows before about 1920. In Winter's study area, the number of grazing animals peaked in 1930, decreased sharply (a 33 percent reduction) until 1935, and increased again until 1951, when a 60 percent reduction was imposed because of severe overgrazing. Since the mid-1960s, the present study area has had approximately 200 cattle grazing for periods of 1-2 months for three consecutive summers followed by a summer of rest from grazing. The field season of 1984 immediately followed the period of grazing in Deer Creek Valley. DCM was laden with cow manure, and the soil was heavily disturbed by cattle hoof prints.

Fire History

Fire records for the three meadows are unavailable, as no fire data are available for the Lemhi Mountains prior to the mid-1960s (Winter 1984). One tree in DCM, however, was fire scarred; a tree-ring core was extracted at the scar, and the year of occurrence was dated at 1938. This fire followed the severe drought of 1934-36, revealed by tree-ring analysis of Douglas fir growing on dry mountain slopes adjacent to the East Fork of the Salmon River (B. R. Butler 1978). Charcoal was recovered from the surface soils in both FM and HM, and was radiocarbon-dated as "modern" (beta 3657 and beta 3655, respectively). Nonetheless, no evidence exists on the surface of these meadows that would indicate extensive fire occurrence.

Nature of Invasion

Approximately five large stumps are located in HM, associated with the construction of a log cabin there. This is the only evidence of tree removal from any of the three meadows, and is not considered to have biased the HM age sampling described below. Small invasive conifers, noticeably smaller than in the surrounding

TABLE 1. Terrain and Soil Characteristics of the Sampled Meadows

Meadow	Elevation, Upvalley end	Elevation, Downvalley end	Meadow Dimensions	Average Slope	Meadow Orientation	Surface soil pH	Color (Dry Munsell)	Texture % Sand	% Silt	% Clay
FM	2,438 m	2,426 m	100mx300m	5°	NE-SW	6.9	10YR 3/3	40	38	22
HM	2,487 m	2,463 m	70mx240m	6-8°	NNE-SSW	7.3	10YR 4/3	48	27	25
DCM	2,365 m	2,347 m	65mx260m	5-7°	NE-SW	7.0	10YR 3/3	47	30	23

TABLE 2. Characteristics of Trees Sampled

Meadow	Total Population	Limber Pine	Lodgepole Pine	Douglas-fir	Subalpine Fir	Engelmann Spruce
First Meadow						
Sample Number	66	6	31	29	0	0
Average Tree Age	64yr	87yr	62yr	61yr	---	---
Average dbh	18cm	22cm	23cm	13cm	---	---
Average Height	9m	11m	11m	6m	---	---
Average Distance from Forest Margin	41.0m	52m	26m	22m	---	---
Harry's Meadow						
Sample Number	32	14	0	10	8	0
Average Tree Age	79 yr	93yr	---	72yr	62yr	---
Average dbh	16cm	12cm	---	25cm	9cm	---
Average Height	8m	7m	---	11m	6m	---
Average Distance from Forest Margin	14.2m	19.m	---	7m	4m	---
Dear Creek Meadow						
Sample Number	23	2	1	11	1	8
Average Tree Age	47yr	79yr	42yr	42yr	47yr	45yr
Average dbh	16cm	11cm	13cm	12cm	6cm	24cm
Average Height	8m	6m	6m	7m	4m	11m
Average Distance from Forest Margin	12.3m	10m	8m	14m	7m	12m

mature forests, dot the surface of each of the three meadows (Figure 2). FM is undergoing the most widespread invasion, and DCM the least. It is these small invasive trees that are the subject of the present study.

Methodology

Tree rings were sampled to determine the period or periods of the onset of tree invasion into the three meadows. A standard increment borer was used to core the invasive trees. Trees were defined as those specimens with a dbh of at least 5 cm, and a height of at least 150 cm.

The main purpose of this study was to determine the period of invasion onset. Young seedlings were, therefore, not sampled. Only one seedling was found in DCM, and less than ten were found in HM. More seedlings are present in FM.

Every tree in HM and DCM (32 and 23, respectively) was cored. The greater number of trees in FM, and time constraints, dictated a more restricted sampling scheme. A sample of 66 trees was cored in FM. All trees were cored in the NE, SE, and SW quadrants of the meadow, where numbers of invasive trees were limited. In the NW quadrant, many invasive trees were present, and a 5 m-wide belt transect was used for sampling. The transect extended from the mature forest margin into the geographic center of the meadow. All trees within the transect were cored.

Every tree was cored 8-10 cm above ground level. A growth factor of 3 yr was added to the total age of each core, following the procedure of Vale (1981b). Cores were stored in plastic straws to protect them during transport. Before counting rings, the cores were dried, mounted, and sanded. Ring counting was done under a 10-60x zoom microscope. Each core was counted twice for accuracy of age determination. The age of establishment for each tree was then categorized by pentad (Figure 3). Species, dbh, estimated height, and distance from the forest/meadow boundary were recorded for each tree sampled.

Results

Average tree age varies considerably among the three meadows (Table 2, Figure 3). Nevertheless, the ages of the invasive trees from all three meadows are considerably younger than mature trees in the surrounding coniferous forest. On the ridge of a nearby well-drained glacial moraine in Mountain Boy Valley, 27 of 35 sampled mature trees cored at breast height exceeded 130 years in age, with 16 of the 35 being more than 200 years old (Butler 1983). On the crest of the moraine which dams FM, a stump (cut during jeep trail construction) revealed 305 annual rings.

Few trees existed in either FM or HM prior to 1880, and none did in DCM (Figure 3). Invasion into FM began in earnest in the mid-1890s, and continued at relatively equal levels until ap-

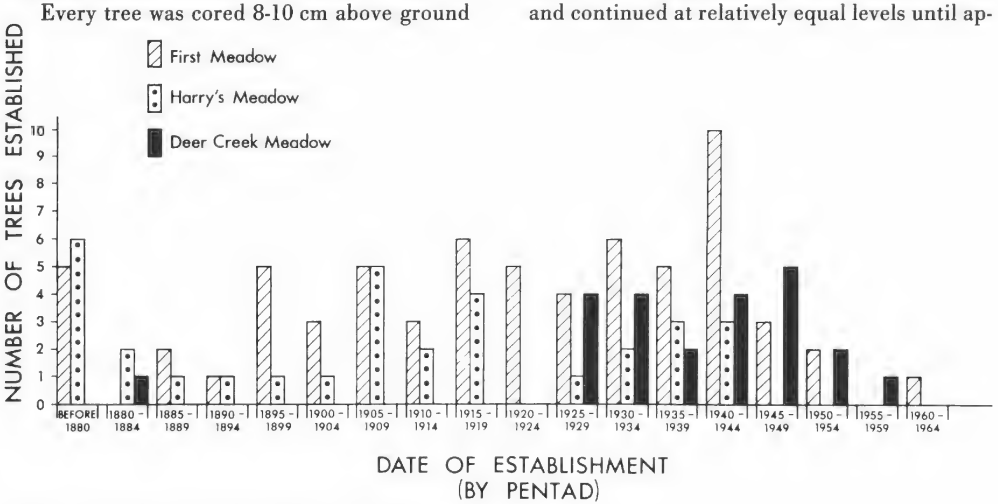

Figure 3. Number of trees established in each meadow, by pentad.

proximately 1950, except for a distinct peak in the early 1940s. Two separate periods of maximum invasion occurred in HM, 1905-1919, and 1925-1945. Invasion has almost ceased in HM, with only the few undated seedlings post-dating 1945. In DCM, all but one tree invaded after 1925, and 55 percent of those invaded after the forest fire of 1938. Invasion ceased after 1959, with only one undated seedling having become established there in the last 25 years.

Definite differences in species age occur in each of the three meadows. In all three, limber pine averages at least 21 years older than the next oldest species. Average age of other species within each individual meadow varies little; only a one year difference between average age of the other two species in FM, and five years or less in DCM (Table 2). Differences in average heights and dbh of sampled trees among the three meadows were not statistically significant. The greater average distance from the mature forest margin in FM may at first glance seem an anomaly, but is accounted for simply by its greater size compared to HM and DCM (Table 1).

Little correlation exists between tree age and height, tree age and dbh, or tree age and distance from forest margin. Simple linear regressions, with tree age as the independent (predictor) variable and tree height (by species within each meadow), tree dbh (by species within each meadow), or distance from forest margin (by species within each meadow) as the dependent variable, were calculated. No R^2 values in excess of 0.25 resulted for the tree age/height, tree age/dbh, and tree age/distance from forest margin calculations; except for a 0.55 R^2 for limber pine dbh as a function of age in FM, and a 0.66 R^2 for subalpine fir distance from forest margin as a function of age in HM. This latter result may be a function of extension into the meadow through sucker-shoot reproduction.

Discussion

Periods of invasion vary among the three meadows, suggesting that 1) no one causal agent is responsible for invasion, or 2) the same causal agent operated at different times in each meadow. Suggestions as to the causal agents in each meadow are outlined below.

In DCM, initial invasion correlates temporally with the dry period of 1920-1940, and with the period of introduction of grazing. Other studies in the region have shown that warmer and drier conditions during these decades produced longer snow-free periods in subalpine meadows, drying the meadow soils and therefore allowing tree invasion (Franklin *et al.* 1971, and Agee and Smith 1984, in the Pacific northwest; Ostler *et al.* 1982, in the Uinta Mountains of Utah; and Schimpf *et al.* 1980, in the northern Wasatch Mountains of Utah). This same period also saw an upper treeline advance at least partially attributable to milder climatic conditions (Winter 1984), so it is reasonable to assign climate as one of the most likely causal agents for the onset of the tree invasion.

Cessation of grazing has been cited as conducive to tree invasion in some studies (Vale 1981a, 1981b), whereas other work suggests that moderate levels of grazing result in abundant tree invasion, by reducing competition with meadow vegetation (Dunwiddie 1977). The introduction of grazing around 1920, at an initially moderate level, probably assisted the establishment of seedlings in DCM. As grazing pressures increased, however, seedling establishment declined except during the immediate post-fire period. Although reduced grazing was recommended in 1950 and imposed in 1951, DCM continues to experience severe grazing disturbance in most summers. This grazing probably precludes continuing invasion of the meadow, in that seedlings are trampled and destroyed before they can become well established and sufficiently large to survive. Cessation of grazing would probably result in a renewed initiation of seedling invasion.

The two periods of pronounced invasion in HM, 1905-1919 and 1925-1945, are probably climate related, with a possible grazing influence in the second period. The first period correlates with the termination of cold, late Neoglacial climatic conditions in the Lemhi Mountains (Knoll 1977, Butler 1983). Snow retention into the summer season was therefore reduced, allowing for the initiation of meadow invasion. The second peak of invasion probably represents a continuation of the invasion process, favored by the drought conditions prevalent in that time period. The onset of grazing in the 1920s may have contributed further to the second phase of invasion.

The period of initial invasion in HM coincides

with the cessation of limber pine establishment in all three meadows, suggesting climate change as the primary invasion instigator. Post-1905 trees in the meadows represent species such as Douglas-fir and lodgepole pine (Table 2), species which are more tolerant of warmer and drier conditions. The limber pine is a tree frequently found near upper treeline (Winter 1984), and is associated with cold climatic conditions. Given the change from late Neoglacial to post-Neoglacial conditions about 1905 in the Lemhis, it is not surprising that limber pine was no longer able to successfully invade and compete in the warmer and increasingly drier meadow environments.

Meadow invasion has essentially ceased in HM, with no tree present (except for the few unsampled seedlings mentioned above) younger than forty years in age (Figure 3). Reasons for this are unclear, in that no grazing has been observed in this meadow in five summer field seasons, nor is the soil of the meadow churned and disrupted as in the heavily-grazed DCM. Fire has not been a factor, nor has human disruption, although a small, sporadically-utilized miner's cabin is located on the fringe of the meadow. No evidence of cutting or stump removal of small trees is present. The total absence of grazing (associated with an absence of seedlings) may lend support to the theory that moderate (but not heavy) grazing levels assist in tree establishment.

Invasion in FM predates the invasion in HM by approximately ten years. In the absence of grazing or fire corroboration, climate remains the most likely causal agent for invasion. FM is more exposed and sunny than HM, and 50 m lower in elevation. These factors may have allowed warming and drying, and subsequent meadow invasion, to begin sooner in FM than in HM.

Once begun, the invasion in FM has remained steady, except for a surge in the 1940-1944 pentad. Although no fire scars were located on trees in FM, the presence of modern charcoal suggests that this surge could be a result of post-fire succession. The large number of invasive lodgepole pine also suggests fire succession. Invasion since the 1940-1944 peak has continued; the decline in number of invasive trees in FM on Figure 3 is an artificial misrepresentation, resulting from the absence of sampling of the many invasive trees which were smaller than the established minimum dbh of 5 cm and height of 150 cm.

Concluding Remarks

Previous studies of invasion of trees into subalpine meadows have cited several possible causal agents. In this study, the influences of these same causal agents have interacted in a complex fashion. Some periods of invasion onset or cessation are attributable to climate changes, whereas others are a result of forest fire succession, or are related to changing grazing pressures interacting with climate change. Each meadow examined had its own unique history, depending on which potential causal agents had interacted in that meadow. Common to all three meadows was the cessation of limber pine establishment around the turn of the 20th century, as milder climatic conditions began to favor the establishment of such species as Douglas-fir, lodgepole pine, and (to a lesser extent) Engelmann spruce and subalpine fir. The climatic causal agent was apparently not limited to the two valleys containing the three study meadows. Climate change was geographically widespread enough to affect meadow establishment in the central portion of the Lemhi Mountains, while at the same time allowing upper treeline expansion to the north and south, over a geographic distance of at least 75 km. Other studies have also shown the geographically widespread distribution of temporally-coincident climate change in the Lemhi Mountains (Knoll 1977, Butler 1984a, 1984b). Reason exists to believe that future climate changes in the area will also be widespread.

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Ectoparasites of *Neotoma cinerea* and *N. fuscipes* from Western Oregon

Abstract

Ectoparasite communities of *Neotoma cinerea* and *N. fuscipes* from western Oregon were described. Mites and fleas occurring on the two hosts were similar whereas the tick and louse communities differed. *Orchopeas sexdentatus, Aplodontopus* sp., *Androlaelaps fahrenholzi,* and *Haemogamasus reidi* were major associates on both hosts. Other important species included *Neohaematopinus inornatus, Echinonyssus neotomae, Miyatrombicula cynos, Neotrombicula cavicola,* and *Euschoengastia oregonensis* on *N. cinerea* and *Myocoptes neotomae* and *Euschoengastia pomerantzi* on *N. fuscipes.*

Introduction

There has been much information published on the ectoparasites of Oregon mammals. Whitaker and Maser (1985) have recently summarized their data on the ectoparasitic and phoretic mites (excluding chiggers) known from Oregon, and information on mites and other parasitic groups has been presented by Hansen (1964), Easton and Goulding (1974), Easton (1975, 1983), Lewis and Maser (1978), Gresbrink and Hopkins (1982), Emerson *et al.* (1984), and Hopkins (1985).

Ectoparasites of the woodrats (*Neotoma* spp.) occurring in the state, however, have not been examined in detail. Whitaker and Maser (1985) reported the occurrence of various laelapid mites on Oregon woodrats, Hubbard (1947) summarized information on their fleas, and Walters and Roth (1950) reported on the invertebrate nest associates of *N. fuscipes* in Oregon. Information on their chiggers and smaller mites is scarce or lacking entirely.

The purpose of this paper is to present information on the ectoparasites of the bushy-tailed woodrat (*Neotoma cinerea*) and the dusky-footed woodrat (*N. fuscipes*) from western Oregon. A third species, occurring only in southeastern Oregon, *N. lepida*, was not examined.

Study Area and Methods

All woodrats were collected from May to October 1984 in the western Cascades province of western Oregon as defined by Franklin and Dyrness (1973). Bushy-tailed woodrats were collected on talus, rock outcrops, and under bridges in the western hemlock (*Tsuga heterophylla*) zone (Franklin and Dyrness 1973) in the vicinity of H. J. Andrews Experimental Forest in Lane and Linn Counties. This area is characterized by a mature Douglas fir (*Pseudotsuga menziesii*) overstory, Pacific rhododendron (*Rhododendron macrophyllum*)-vine maple (*Acer circinatum*) understory, and salal (*Gaultheria shallon*)-Oregon grape (*Berberis nervosa*) ground cover. Dusky-footed woodrats were collected at their stick houses near Tiller, Douglas County. This area lies within the mixed conifer zone (Franklin and Dyrness 1973) and is characterized by a Douglas fir overstory, Pacific madrone (*Arbutus menziesii*) understory, and Pacific poison oak (*Rhus diversiloba*) ground cover.

Ectoparasites were removed from the fur with the aid of a dissecting microscope, a fine probe, and forceps. Follicular mites and other imbedded forms were forced from the skin with fine forceps. After manual inspection, animals were processed with a washing technique (Whitaker 1982) to collect any additional parasites. All ectoparasites were preserved in 70 percent ethanol, cleared and stained in Nesbitt's solution, and mounted in Hoyer's solution for later identification.

Results and Discussion

At least 44 ectoparasitic and phoretic species were found on Oregon woodrats (Table 1). Mites were best represented with 32 species, followed by fleas (6 species), ticks (5 species), and lice (1 species). Although fewer *Neotoma cinerea* were examined (N = 30 vs 35), this species harbored

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TABLE 1. Ectoparasites of the woodrats, *Neotoma cinerea* and *N. fuscipes*, from western Oregon

	Neotoma cinerea (N = 30)				*Neotoma fuscipes* (N = 35)			
	Occurrence		Number		Occurence		Number	
	No.	%	Total	Av.	No.	%	Total	Av.
Siphonaptera								
Anomiopsyllus falsicalifornicus congruens					3	9	6	0.2
Atyphloceras multidentatus multidentatus	4	13	6	0.2	2	6	2	0.1
Ceratophyllus (Amonopsyllus) ciliatus protinus	1	3	1	<0.1				
Megarthroglossus procus procus	2	7	7	0.2	4	11	5	0.1
Orchopeas sexdentatus cascadensis	28	93	240	8.0	32	91	207	5.9
Rhadinopsylla (Micropsylla) sectilis goodi	1	3	1	<0.1				
Anoplura								
Neohaematopinus inornatus	8	27	159	5.3				
Acarina								
Ixodidae								
Dermacentor occidentalis	3	10	4	0.1	11	31	66	1.9
Ixodes angustus	8	27	10	0.3				
I. ochotonae	1	3	1	<0.1				
I. pacificus	4	13	10	0.3	1	3	1	<0.1
I. spinipalpis					7	20	28	0.8
Acaridae								
Tyrophagus sp.					1	3	1	<0.1
Anoetidae								
anoetid (?)	1	3	120	4.0				
Ascidae								
Proctolaelaps sp.	1	3	2	0.1	2	6	5	0.1
Cheyletidae								
Cheyletus sp.	3	10	3	0.1				
Eucheyletia bishoppi	3	10	9	0.3				
Chortoglyphidae								
Aplodontopus sp.	12	40	5076	169.2	35	100	28647	818.5
Cyrtolaelapidae								
Cyrtolaelaps sp.	1	3	9	0.3				
Euryparasitus sp.	1	3	2	0.1	1	3	1	<0.1
Glycyphagidae								
Dermacarus spermophilus	2	7	4	0.1	7	20	41	1.2
Xenoryctes sp. near *nudus*					2	6	11	0.3
Laelapidae								
Androlaelaps casalis	1	3	1	<0.1				
A. fahrenholzi	17	57	87	2.9	12	34	57	1.6
Echinonyssus neotomae	11	37	152	5.1				
E. obsoletus	1	3	1	<0.1				
E. utahensis	2	7	9	0.3				
Eulaelaps stabularis					1	3	1	<0.1
Haemogamasus reidi	11	37	85	2.8	14	40	91	2.6
Hypoaspis lubrica	3	10	5	0.2	1	3	4	0.1
Myobiidae								
Radfordia neotomae	6	20	73	2.4	7	20	20	0.6
Myocoptidae								
Myocoptes neotomae	2	7	11	0.4	17	49	119	3.4
Pygmephoridae								
Bakerdania sp.	1	3	10	0.3	2	6	2	0.1
Pygmephorus whitakeri	1	3	1	<0.1				
Trombiculidae								
Chatia setosa	8	27	16	0.5	1	3	1	<0.1
Comatacarus americana					2	6	3	0.1
Euschoengastia oregonensis	14	47	88	2.9				
E. peromysci	7	23	55	1.8	6	17	22	0.6
E. pomerantzi	4	13	31	1.0	10	29	165	4.7
E. simulans					5	14	15	0.4
Miyatrombicula cynos	2	7	305	10.2				
Neotrombicula cavicola	16	53	108	3.6	1	3	3	0.1
N. microti	5	17	37	1.2				

a more diverse ectoparasite community (37 species) than *N. fuscipes* (27 species).

Fleas

Orchopeas sexdentatus cascadensis was the most abundant flea on both woodrats. The species is the major flea of the entire genus *Neotoma*. The wandering habits of woodrats, their associations with other hosts, and the fact that they spend a significant amount of time in their nests make them susceptible to a wide diversity of fleas, often in great numbers (Hubbard 1947). *Neotoma cinerea* and *N. fuscipes* are host to more than 50 species of fleas throughout their range. Of the fleas recorded in the present study, only *Rhadinopsylla sectilis goodi* and *Ceratophyllus* (*Amonopsyllus*) *ciliatus protinus* were not reported by Hubbard (1947) or Easton (1983) for these hosts. *Rhadinopsylla sectilis goodi* is a parasite primarily of deer mice (*Peromyscus maniculatus*) and ground squirrels (*Spermophilus* spp.), while most members of the genus *Ceratophyllus* are parasitic on tree and ground squirrels in western North America (Smit 1983).

Lice

A single species, *Neohaematopinus inornatus*, was quite common on *N. cinerea* and has previously been reported from this host in Oregon (Hansen 1964, Emerson *et al.* 1984). *Neohaematopinus neotomae* has been reported from *N. fuscipes* in California (Linsdale and Tevis 1951) but no lice were found on this host during the present study.

Ticks

The most common ticks were *Ixodes angustus* and *I. pacificus* on *N. cinerea* and *Dermacentor occidentalis* and *Ixodes spinipalpis* on *N. fuscipes*. Easton and Goulding (1974) reported *I. angustus* from both hosts and *I. pacificus* from *N. fuscipes* in western Oregon. The occurrence of *Ixodes ochotonae* is a new record for Oregon although it has previously been reported from California and Washington.

Mites

The most important mites (> 1.0 per host) on *N. cinerea* were, in descending order of abundance, *Aplodontopus* sp., *Miyatrombicula cynos, Echinonyssus neotomae,* an anoetid (?), *Neotrombicula cavicola, Euschoengastia oregonensis, Androlaelaps fahrenholzi, Haemogamasus reidi, Radfordia neotomae, Euschoengastia peromysci, Neotrombicula microti,* and *Euschoengastia pomerantzi.* Major associates of *N. fuscipes* were *Aplodontopus* sp., *Euschoengastia pomerantzi, Myocoptes neotomae, Haemogamasus reidi, Androlaelaps fahrenholzi,* and *Dermacarus spermophilus.*

State distribution records for Oregon included *Aplodontopus* sp., *Xenoryctes* sp. near *nudus, Hypoaspis lubrica, Radfordia neotomae,* and *Myocoptes neotomae.* Members of the genus *Aplodontopus* are small elongate mites collected from the hair follicles of the tails of woodrats, some ground squirrels, and the mountain beaver (*Aplodontia rufa*). Those found on woodrats are the deutonymphal stage of a possibly undescribed adult chortoglyphid found only in the nest of the host. Their status is currently under study. *Hypoaspis lubrica* has been reported from a wide variety of hosts throughout the United States (Whitaker and Wilson 1974). *Radfordia neotomae* was originally described from *N. fuscipes* in California (Jameson and Whitaker 1975), but males have not previously been collected or described. *Myocoptes neotomae* has been collected on *N. floridana* in Indiana (Cudmore, in press) and was recently described as a new species from that host (Fain *et al.* 1983). *Xenoryctes* sp. near *nudus* and Anoetidae (?) may represent new species and are also under investigation.

Ectoparasites not previously reported for these hosts included *Aplodontopus* sp., *Eucheyletia bishoppi, Androlaelaps casalis, Echinonyssus obsoletus, E. utahensis, Radfordia neotomae,* and *Pygmephorus whitakeri* for *N. cinerea, Xenoryctes* sp. near *nudus* and *Eulaelaps stabularis* for *N. fuscipes*, and *Dermacarus spermophilus, Hypoaspis lubrica,* and *Myocoptes neotomae* for both species. Easton (1975) reported the chiggers, *Miyatrombicula cynos, Neotrombicula harperi,* and *N. cavicola* from *N. cinerea* and *Neotrombicula cavicola* from *N. fuscipes* collected in western Oregon.

If incidental forms are eliminated (*i.e.* one or two occurrences on either host), the ectoparasite communities of these two hosts are quite similar: 17 species in common, 6 unique to *N. cinerea,* and 3 unique to *N. fuscipes. Aplodontopus* sp.,

Myocoptes neotomae, and *Radfordia neotomae* are restricted to the genus *Neotoma* and were found on both hosts.

Most notable among the differences between the ectoparasite communities of these two hosts were the presence of 1) three species of *Echinonyssus* on *N. cinerea,* none on *N. fuscipes*; 2) *Ixodes angustus* only on *N. cinerea, I. spinipalpis* only on *N. fuscipes*; 3) *Neohaematopinus inornatus* only on *N. cinerea;* and 4) *Euschoengastia oregonensis* and *Neotrombicula microti* only on *N. cinerea, Euschoengastia simulans* and *Comatacarus americana* only on *N. fuscipes.*

In Oregon, *N. fuscipes* occurs in the Willamette Valley north to the Columbia River and throughout much of southwestern Oregon, whereas *N. cinerea* is nearly ubiquitous. Although their ranges overlap extensively in southwestern Oregon, *N. cinerea* is most closely associated with northern conifer forest types (especially in rocky habitat), whereas *N. fuscipes* is most closely associated with southern brushy chaparral vegetation types (Maser *et al.* 1981). Some differences in the ectoparasite communities of these two hosts may, therefore, be the result of differences in habitat rather than host preference of the parasites. This may be particularly true for some chiggers which are often described as habitat specific rather than host specific.

The taxonomic affinities of *N. cinerea* and *N. fuscipes* are not clear. Earlier authors (Merriam 1894, Goldman 1910) believed these two species to be widely divergent and placed them in separate subgenera. Burt and Barkalow (1942) also supported separation at the subgeneric level based on bacular differences. A more recent investigation however (Carleton 1980), suggested that *N. fuscipes* and *N. cinerea* share a common ancestry and may be more closely related than previously believed. Ectoparasite community similarities would seem to support this contention; however, comparable data are lacking for most other *Neotoma* species.

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Water Relations of Two Subspecies of Big Sagebrush on Sand Dunes in Southeastern Idaho.

Abstract

Distributions of two subspecies of big sagebrush (*Artemisia tridentata* Nutt. subspecies *tridentata* and *A. tridentata* Nutt. subspecies *wyomingensis*) are associated with a soil texture gradient at sand dunes in southeastern Idaho. The two subspecies co-occur at the middle of the gradient on dune margins. The present study compared plant and soil water potentials among dune tops, dune margins, and adjacent slacks. We tested the hypothesis that there were no differences in these measured variables among the three locations on the dune landscape. Soil water potentials on the dune margins were significantly less negative then those on the adjacent slacks. Soil water potentials on the dune tops were not significantly different from those on the dune margins or the slacks. Predawn and midday plant water potentials of subspecies *tridentata* on the dune tops and both subspecies on the dune margins were significantly less negative than those of subspecies *wyomingensis* on the slacks. There was no difference in plant water potential between the two subspecies growing together on the dune margins. Plant water potentials of the two subspecies were significantly different when soil water potentials associated with each subspecies were also significantly different, even though subspecies *tridentata* plants were larger than subspecies *wyomingensis* plants.

Introduction

Inland sand dunes in arid and semiarid regions of North America have relatively moist soil environments compared to adjacent, fine textured soils (Barnes and Harrison 1982, Bowers 1982, Chadwick and Dalke 1965, Kirkpatrick and Hutchinson 1980, Pavlik 1980, Tevis 1958). Coarse textured sands have more macropores, which allow water from precipitation to infiltrate with little runoff or evaporation. Fine textured soils with high water holding capacities have surface layers that become saturated, resulting in surface evaporation and runoff. Thus, more water from precipitation is available to plants in the sandy soil on dunes than in adjacent, fine textured soils (Barnes and Harrison 1982, Bowers 1982, Pavlik 1980).

Distributions of two subspecies of big sagebrush at the Idaho National Engineering Laboratory (INEL) in southeastern Idaho are associated with a gradient in soil texture (Shumar 1983). Basin big sagebrush (*Artemisia tridentata* Nutt. subspecies *tridentata;* Beetle 1960) occurs on sandy areas and sand dunes and Wyoming big sagebrush (*Artemisia tridentata* Nutt. subspecies *wyomingensis;* Beetle and Young 1965) occurs on adjacent, fine textured soils. However, the subspecies co-occur along the dune margins, which are areas with shallow sand accumulation at the middle of the soil texture gradient.

Barker and McKell (1983) examined the water relations of the two sagebrush subspecies in contiguous stands, but on different soils. They found significantly lower soil and plant water potentials associated with Wyoming big sagebrush. However, Miller *et al.* (1982) found that soil and plant water relations of basin big sagebrush and Wyoming big sagebrush on separate sites were not significantly different. The presence of pure and mixed stands of the subspecies along the soil texture gradient at the INEL provided the opportunity to resolve the question of whether the two sagebrush subspecies have similar water relations when growing on the same soil or have some genetically determined difference that precludes similar water relations.

The present study compared plant and soil water potentials among dune tops, dune margins, and slacks (area between dunes with silt loam soil and no loose sand). The null hypotheses tested were: 1) soil water potentials are the same among the three areas of the sand dune environment, 2) plant water potentials are the same between basin big sagebrush plants on the dune tops and Wyoming big sagebrush plants on the slacks, and 3) plant water potentials are the same for both subspecies when they are growing together on the dune margins.

Methods and Materials

Plant and soil water potentials were measured at linear-type, stabilized sand dunes (*cf.* McKee 1982) during the summer of 1982. Three replicate transects were established, each extending from the top of a dune to the adjacent slack. Precipitation and other meteorological characteristics were assumed to be equal for all three transects at any particular time because these transects were within 250 m of each other.

Screen-caged thermocouple psychrometers (J. R. D. Merrill Co., Logan, Utah) were placed in the soil at the dune top, dune margin, and the slack at each transect. Because of a limited supply, one psychrometer was placed at one depth at each location on the dune landscape. This depth was subjectively determined by estimating the zone of maximum water accumulation in each case based on soil characteristics. At the slacks, the psychrometers were placed at a depth of 45 cm, which corresponded to the depth of an indurant layer of clay and calcium. We surmised that little available water would be found below this layer. At the margins, psychrometers were placed between 50 and 60 cm, which is the approximate depth of the interface between the sand and the underlying loess. We assumed that water would accumulate at these interfaces between different soil textures (Brady 1974, p. 186). Examination of the soil profile showed the highest density of roots in the same region. Psychrometers were placed approximately 75 cm deep at the dune tops. This depth was determined to be the average depth of roots by digging a trench and examining the root distribution.

Psychrometers were measured at midmorning on the following dates: 12 June, 27 June, 16 July, 30 July, 14 August, 4 September, and 5 October. The procedures and computer program of Brown and Bartos (1982) were used to determine soil water potential from psychrometer microvolt output.

Plant water potential was measured before dawn on the same dates psychrometer readings were taken, at midday on those dates except for 5 October, and diurnally at 2-hr intervals on 12 June and 16 July. Plant water potential was measured with a pressure bomb (Waring and Cleary 1967) on sagebrush branches clipped from the sunlit portion at the top of the crown. At each transect, four plants were selected for water potential measurements; a basin big sagebrush plant at the dune top, a Wyoming big sagebrush plant at the slack, and one plant of each subspecies at the dune margin. Plants were randomly selected within a 5 m radius of each soil psychrometer. The same plants were used for predawn, midday, and diurnal measurements for the duration of the experiment. Because there were three transects, the sampling regime provided three measurements of plant water potential for each landscape position and subspecies. Estimates of between plant variance were measured on adjacent plants at approximately the same time in a previous study (95 percent confidence intervals were ± 0.5 Mpa for basin big sagebrush and ± 0.2 Mpa for Wyoming big sagebrush).

Soil water potential was analyzed with a two-way analysis of variance, with date as a random factor and position on the dune landscape (*i.e.* dune tops, dune margins, and slacks) as a fixed factor. Predawn and midday plant water potentials were analyzed by three-way analysis of variance, with date as a random factor and landscape position and subspecies as fixed factors. The alpha level was set at 0.05 for all tests. If the analyses of variance indicated significant differences among landscape positions or subspecies, then the Student-Newman-Keuls (SNK) multiple range test was used to determine which landscape positions or subspecies were significantly different from the others.

Results

The two-way analysis of variance of soil water potential indicated that the main effects, date and landscape position, were both significant. A subsequent SNK showed that the margins had significantly less negative water potentials than the slacks (Figure 1). Soil water potential at the dune tops was not significantly different from that of the margins or the slacks. Figure 1 shows that soil water potential on the dune tops was less negative than that of the margins in June, but dropped rapidly to a level similar to that of the slacks by the end of July.

Significant main effects in the three-way analysis of variance showed that predawn and midday plant water potentials were significantly different among dates, landscape positions, and subspecies. A significant two-way interaction between landscape positions and subspecies and a subsequent SNK analysis indicated that predawn

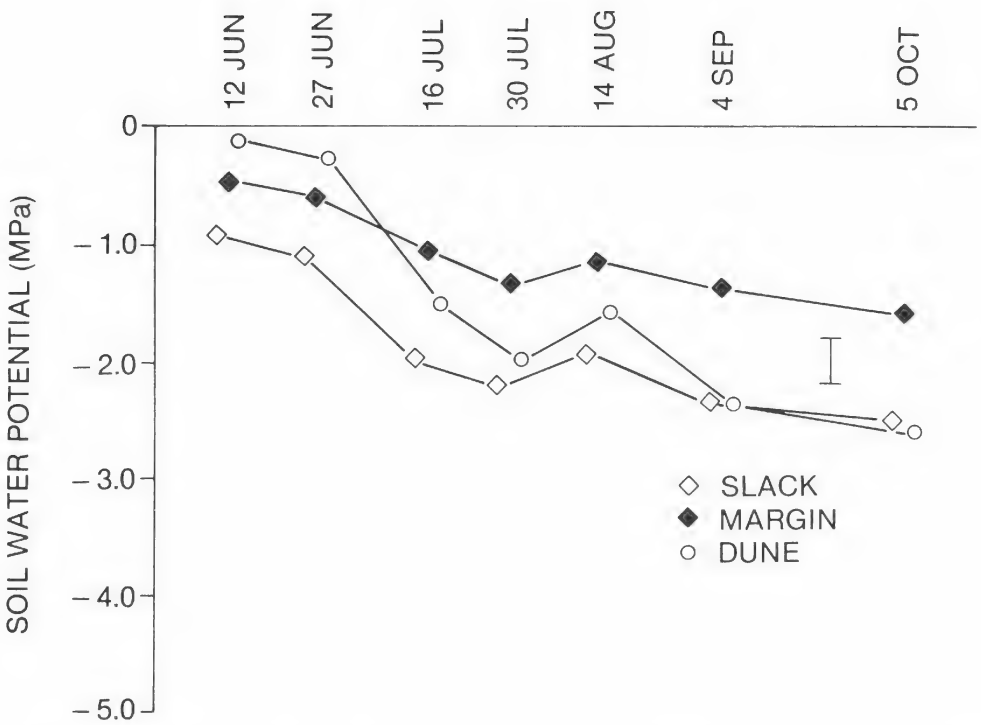

Figure 1. Average soil water potential at the slacks, dune margins and dune tops (labeled slack, margin and dune respectively) measured on seven dates in 1982. Values for the margins are significantly ($P < 0.05$) less negative than those of the other two landscape positions. Standard error bar is shown on the figure between 4 September and 5 October values.

water potential of Wyoming big sagebrush at the slacks was significantly more negative than predawn water potentials of big sagebrush at the dune tops and both subspecies at the margins (Figure 2). Predawn plant water potentials were not significantly different among the two subspecies at the margin and basin big sagebrush at the dune tops (Figure 2). Midday plant water potentials showed the same differences as predawn plant water potentials. Midday water potential of Wyoming big sagebrush at the slacks was significantly more negative than midday water potentials of basin big sagebrush at the dune tops and both subspecies at the margins (Figure 2).

The magnitudes of the difference between mean predawn and mean midday water potential were similar among landscape positions and subspecies on most dates. These daily differences ranged from a low of 0.3 MPa change in June to a maximum change of 1.4 MPa in August. Diurnal fluctuations in plant water potential for plants at the three landscape positions on 12 June and 16 July are presented in Figure 3. Diurnal patterns were similar for all plants on the slacks, margins, and dune tops. Water potentials of Wyoming big sagebrush plants at the slacks were consistently more negative than that of plants at the other two locations. Plant heights averaged 1.38 m and 0.81 m for basin big sagebrush and Wyoming big sagebrush respectively (Figure 3).

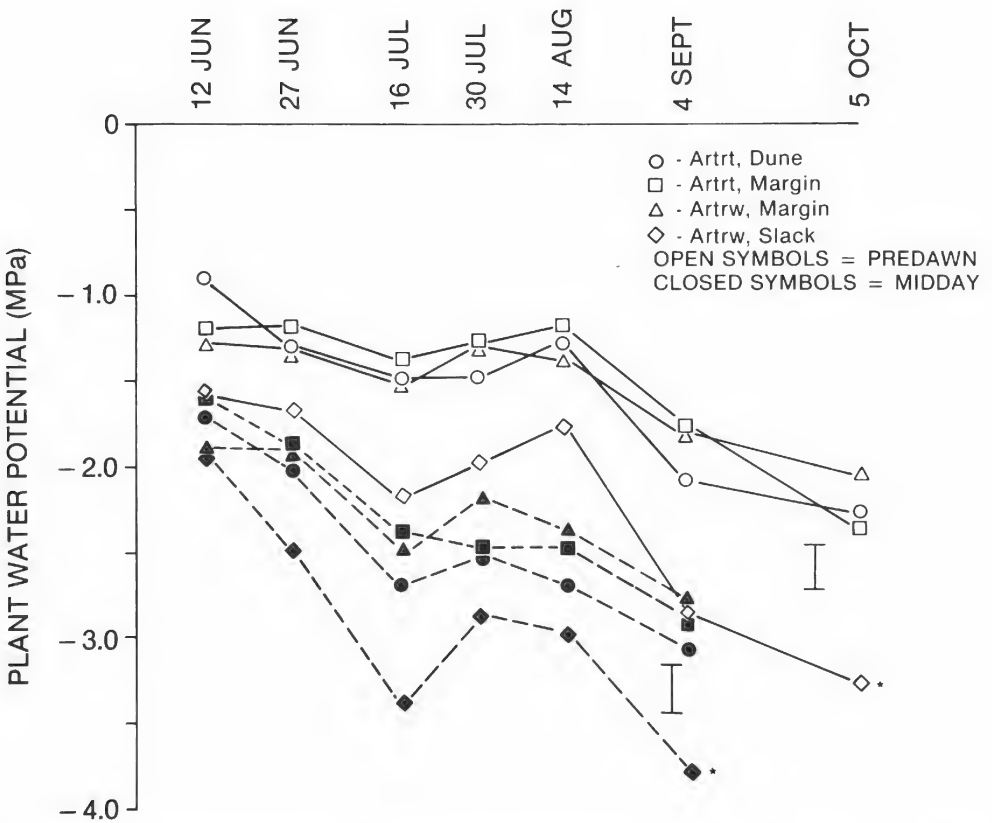

Figure 2. Predawn and midday plant water potential for basin big sagebrush (Artrt) on the dune, Wyoming big sagebrush (Artrw) on the slack, and both subspecies on the margin (see figure inset). Water potentials (both predawn and midday) for Wyoming big sagebrush on the slack (*) are significantly ($P < 0.05$) more negative than those of basin big sagebrush on the dune and both subspecies on the margin. Standard error bars for predawn and midday values are depicted on the figure.

Discussion

Plant water potentials of the subspecies were different only when soil water potentials associated with each subspecies were also significantly different. Plant water potentials of the two subspecies did not differ from each other when plants were growing on the same soil (*i.e.*, dune margins, Figure 2). Both predawn and midday water potentials of Wyoming big sagebrush on the slacks were considerably lower than those of basin big sagebrush on the dune tops and both subspecies on the margins (Figure 2). Soil water potentials were also lower on the slacks than on the margins (Figure 1). Despite genetically controlled differences in root and shoot size between the two subspecies, they do not appear to respond differentially to soil water availability.

The results of Miller *et al.* (1982) and Barker and McKell (1983) also suggest that predawn plant water potentials of both sagebrush subspecies were similarly affected by soil water potentials. Miller *et al.* (1982) and our results indicate that the magnitude of the fluctuation be-

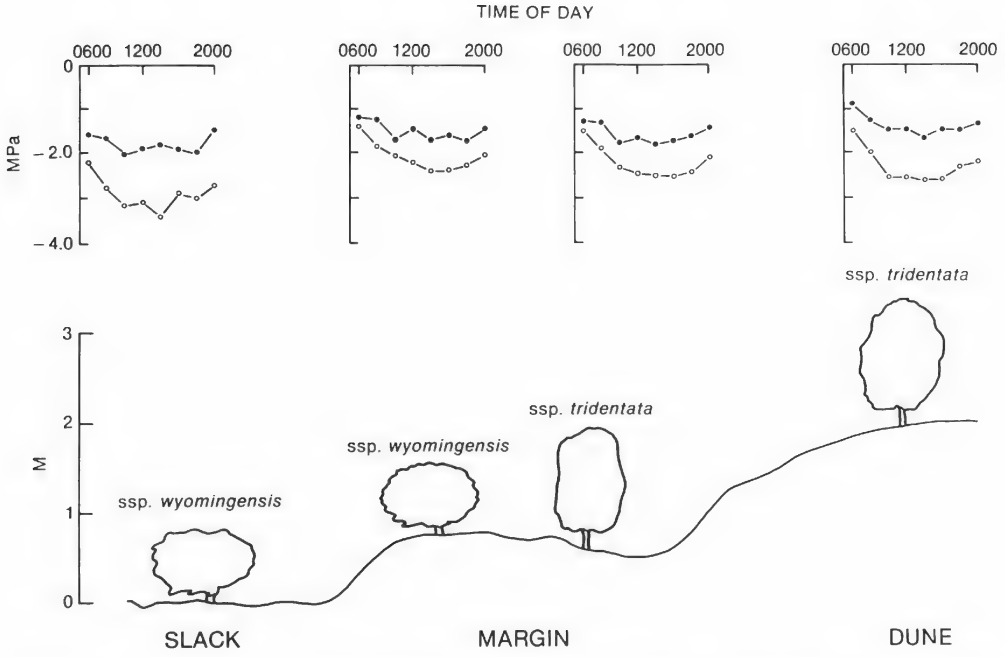

Figure 3. Diurnal curves of plant water potential taken on 12 June (closed circles) and 16 July (open circles). Curves correspond with the respective sagebrush subspecies and their location as depicted for the dune study area in the lower portion of the figure. Plants and dune landscape are scaled to average heights (m).

tween predawn and midday water potentials was about the same for the two sagebrush subspecies on any one date, which suggests that these midday values were affected by the evaporative demands of the day and the predawn value. The predawn value reflects soil water availability. Barker and McKell (1983) found differences in plant water potential between these two subspecies on three of six dates. Soil water potential under the respective subspecies were also significantly different on those dates.

Miller *et al.* (1982) found no differences in either predawn or midday water potentials between basin big sagebrush on one site and Wyoming big sagebrush on a second. The authors indicate that the deeper soils supporting basin big sagebrush held more water than the shallow soils supporting Wyoming big sagebrush. They attributed the similarity in plant water potentials of the two subspecies to higher "transpiration potentials" of basin big sagebrush because of its greater leaf area. Thus, although more water was available to basin big sagebrush, its leaf water potentials were similar to those of Wyoming big sagebrush because of higher transpiration. Our results indicate that basin and Wyoming big sagebrush had similar water potentials despite differences in size of the plants on the dune margin. We suspect that basin big sagebrush plants would have a larger root volume in addition to a greater leaf area. Thus, the root/shoot ratios may have been similar between the subspecies, resulting in equal plant water potentials so long as soil water content in the root zones and transpiration resistances were equal between the two stands. Barker and McKell (1983) found no differences in transpiration resistances between these two subspecies.

Predawn plant water potentials were not different between the dune tops and the margins, suggesting that more water was available below the depth where the psychrometers were located at the dune tops. Psychrometers at the dune tops

were placed at a depth of 75 cm, even though sand depth was as much as 200 cm. Although a high density of roots is found above 70 cm, big sagebrush plants commonly have roots that extend to 180 cm (Sturges 1977). We suspect that psychrometers at the dune tops were not deep enough to detect maximum water availability; had they been placed deeper, soil water potentials would probably have been similar between the margins and dune tops.

Increases in soil and plant water potentials during August were probably the result of precipitation inputs. From 16 July to 30 July, soil water potentials decreased (Figure 1) but plant water potentials increased (Figure 2). This apparent discrepancy may have been due to precipitation that wet the upper horizons of the soil in contact with plant roots but did not infiltrate down to the level of the psychrometers. Alternatively, the higher plant water potentials on 30 July as compared to 16 July also may have resulted from the loss of ephemeral leaves that generally occurs in July (Depuit and Caldwell 1973). Abrupt reductions in shoot/root ratios occur in other desert plants to the benefit of the plant's water status (Etherington 1982).

Diurnal patterns of water potentials for big sagebrush in this study were similar to those of Depuit and Caldwell (1973), Everett *et al.* (1977), and Campbell and Harris (1977). Minimum water potentials were −3.9 MPa for Wyoming big sagebrush and −3.5 MPa for basin big sagebrush, and were similar to minimum values reported by Depuit and Caldwell (1973) and Miller *et al.* (1983). Although Branson *et al.* (1976) and Everett *et al.* (1977) obtained minimum values considerably lower than ours, Campbell and Harris (1977) obtained values similar to ours during a wet year and values similar to those of Branson *et al.* (1976) and Everett *et al.* (1977) during a dry year. These results provide additional support to our hypothesis that plant water potential of the two subspecies is directly affected by soil water potential.

Higher moisture availability in dune sand as opposed to finer textured soils is in agreement with the work of other investigators (Barnes and Harrison 1982, Bowers 1982, Chadwick and Dalke 1965, Kirkpatrick and Hutchinson 1980, Pavlik 1980, Tevis 1958). Pavlik (1980) and Barnes and Harrison (1982) also reported higher water potentials of plants on sand dunes as compared to plants on adjacent non-dune substrates.

Conclusions

The dune margins were more mesic than the slacks. The phenomenon of moisture retention in the stabilized sand dunes at the INEL is similar to that reported for other inland sand dunes in the arid and semiarid regions of the American West. Water potential of basin big sagebrush plants at the dune tops and plants of both subspecies at the margins were significantly less negative than that of Wyoming big sagebrush plants at the slacks. There was no difference in plant water potential between the two subspecies growing together on the margins. The subspecies differ in size but apparently do not differ physiologically with respect to water potential.

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Bald Eagle Perch-sites in Eastern Washington

Abstract

We monitored Bald Eagle (*Haliaeetus leucocephalus*) use and relative abundance of perch types along major water bodies in eastern Washington during the winters of 1982-83 and 1983-84. Eagles perched in ponderosa pines (*Pinus ponderosa*), snags, cottonwoods (*Populus* spp.), man-made structures, the ground, ice, and other sites. Use of perches varied with their availability along each water body. Ponderosa pines, snags, and cottonwoods received high proportions of use where they were available. Bald Eagle perches should be considered in the management of riparian areas.

Introduction

Wintering Bald Eagles (*Haliaeetus leucocephalus*) spend much of each day perching (Servheen 1975). The availability of suitable perches may influence the local distribution of wintering Bald Eagles (Erickson *et al.* 1976, Stalmaster and Newman 1979, Fielder and Starkey 1980, Steenhof *et al.* 1980).

More than 200 Bald Eagles annually winter along the major water bodies in eastern Washington. Shorelines along eastern Washington water bodies offer a variety of perch types. However, these shorelines are also subject to extensive human modification (*e.g.*, logging, firewood cutting, livestock grazing, and hydroelectric, agricultural, residential, recreational, and highway development and expansion). Steenhof *et al.* (1980) found that 58 percent of the Bald Eagles wintering in South Dakota perched within 5 m of the water. Therefore shoreline modifications may affect wintering Bald Eagles. Wildlife managers should consider the availability and importance of those perches to bald eagles when evaluating shoreline modifications. To facilitate this consideration, and supplement Bald Eagle perch site information for western Washington (Stalmaster and Newman 1979), we present information of 1336 observations of Bald Eagles perched or flying along the water bodies in eastern Washington.

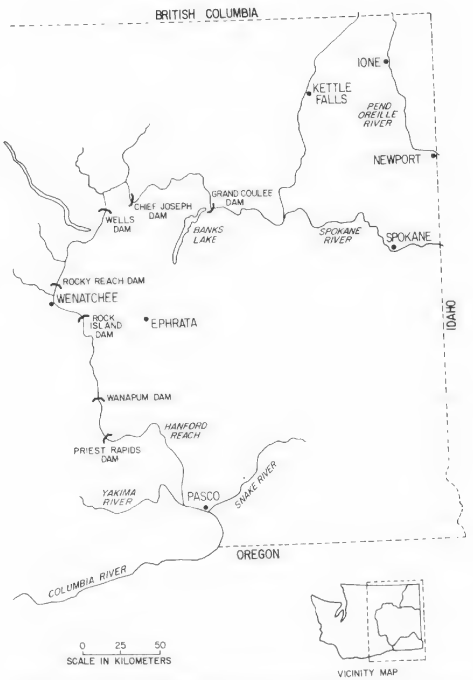

Figure 1. Eastern Washington Bald Eagle survey area.

Study Area

The study area (Figure 1) included the Columbia River (from Pasco to about 10 km above Kettle Falls), Banks Lake, the Spokane River (from

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its mouth to Spokane), and the Pend Oreille River (from Newport to Ione), a total of 1775 km of shoreline. We divided the study area into segments because of their management by a variety of hydroelectric agencies. We addressed the Columbia River according to the reservoirs lying behind the hydroelectric dams (Priest Rapids, Wanapum, Rock Island, Rocky Reach, Wells, and Chief Joseph). The Hanford Reach included the Columbia River between Pasco and Priest Rapids Dam. FDR Reservoir, lying behind Grand Coulee Dam, was divided into south FDR Reservoir (the Columbia River between the dam and the mouth of the Spokane River) and north FDR Reservoir (the portion between the Spookane River mouth and 10 km upstream from Kettle Falls). The Spokane and Pend Oreille rivers were each treated as separate segments.

The study area included 5 vegetation associations or zones described by Franklin and Dyrness (1973): the *Artemisia tridentata-Agropyron spictatum* and *Artemisia tripartita-Festuca idahoensis* vegetation associations and the *Pinus ponderosa, Tsuga heterophylla* and *Pseudotsuga menziesii* zones. The physical character of the study area shorelines also varied greatly (*e.g.,* arid lands, gravel bars, mud flats, steep basalt cliffs, and forests).

Vegetation or shoreline characteristics along several segments merit discussion. The Hanford Reach has many large cobble islands and several stands of black locust (*Robinia pseudoacacia*) and Chinese elm (*Elmus* sp.) trees. Very tall basalt cliffs border most of the southern 2/3 of Wanapum Reservoir. Man-made raptor perches, designed for Bald Eagles, have been erected along Wanapum, Rock Island, Wells, and Chief Joseph reservoirs. Except for 4 tripods with crossarms along Rock Island Reservoir, all man-made perches along these reservoirs are single poles with crossarms. A large number of river pilings occur in the Pend Oreille River and these power poles, and towers were also classified as man-made perches. Much of Banks Lake is bordered by steep basalt cliffs. Banks Lake, large portions of the Spokane River, and large embayments along the Pend Oreille River freeze over each winter. Most of the remainder of the study area remains relatively ice-free.

Methods

Observations of Bald Eagles, and their perches were recorded monthly from November 1982-February 1983 and November 1983-March 1984, except the Spokane and Pend Oreille rivers were not surveyed during the winter of 1982-83.

Surveys were conducted in a high-wing Cessna aircraft, flown at speeds of 130-145 km/h, 30-60 m above ground level, using an observer/pilot and at least one additional observer. The same direction was flown each month within five days of the 15th of each month, except when weather reduced visibility. Where river or reservoir width exceeded 0.8 km, each shoreline was flown separately because eagle sightings were more easily made within a distance of 0.4 km from the aircraft. Where water body widths were 0.8 km or less, the route was flown along the center axis of the water, allowing both shores to be observed simultaneously.

In recording perches, the use of dead portions of a tree was included with snag use. Ground perches included cliffs, shoreline rocks, mud flats, and gravel bars. We included counts of flying birds as part of Table 1 for comparative purposes.

We used rank correlation (Chapman and Schaufele 1970) to analyze availability and use of perch types along each water body. Subjective ranking of the relative availability of perch types allowed comparison of numbers of trees, lengths of cliffs, and areas of gravel bars and ice.

Results and Discussion

Bald Eagles used perch sites in eastern Washington primarily according to their varying availability along the water bodies surveyed. Of the 1336 Bald Eagle sightings tallied during nine surveys (four of which did not include the Spokane and Pend Oreille rivers), 14 percent were of eagles in flight which had not been flushed by our approach. They were either soaring or in transit. Along the mainstem Columbia (two winters of surveys) Bald Eagles perched in ponderosa pines, snags, on the ground and in cottonwoods 34 percent, 26 percent, 15 percent, and 12 percent of the time, respectively (Table 1). Along the Spokane and Pend Oreille rivers, (one winter of surveys) eagles perched in ponderosa pine, cottonwoods and snags 32 percent, 27 percent and 24 percent of the time, respectively.

TABLE 1. Utilization of bald eagles perch sites along major water bodies in eastern Washington (number of sightings is followed by percent of sightings in parentheses).

Body of water[1]	Ponderosa pine	Snag	Cotton-wood	Man-made structure	Other[2]	Ground[3]	Ice	Total	No. Flying
Hanford Reach	0(0)	3(3)	6(5)	4(3)	Rp 78(67)	G 26(22)	0(0)	117	12
Priest Rapids Res.	0(0)	1(8)	5(38)	0(0)	Jo 1(8)	G 6(46)	0(0)	13	5
Wanapum Res.	0(0)	0(0)	0(0)	0(0)	Rp 1(3)	C 31(97)	0(0)	32	13
Rock Island Res.	0(0)	1(20)	3(60)	1(20)	0(0)	C 0(0)	0(0)	5	1
Rocky Reach Res.	15(32)	15(32)	11(23)	0(0)	Pm 3(6)	C 3(6)	0(0)	47	9
Wells Res.	13(17)	18(24)	32(43)	3(4)	Pm 6(8)	G 3(4)	0(0)	75	0
Chief Joseph Res.	46(47)	43(44)	2(2)	1(1)	Pm 3(3)	C 2(2)	0(0)	97	3
Banks Lake	18(10)	27(16)	65(38)	0(0)	Pm 1(1)	C 57(33)	4(2)	172	58
South FDR Res.	34(40)	26(30)	1(1)	0(0)	Pm 12(14)	C 13(15)	0(0)	86	12
North FDR Res.	226(57)	136(34)	4(1)	0(0)	Pm 13(3)	G 17(4)	0(0)	396	57
	352(34)	270(26)	129(12)	9(1)	118(11)	158(15)	4(<1)	1040	170
Spokane R.	32(48)	20(30)	0(0)	0(0)	Pm 6(9)	C 4(6)	4(6)	66	6
Pend Oreille R.	4(9)	7(15)	30(65)	4(9)	Pm 0(0)	G 0(0)	1(2)	46	8
	36(32)	27(24)	30(27)	4(4)	6(5)	4(4)	5(4)	112	14

[1]Spokane and Pend Oreille rivers were surveyed 5 times, other water bodies were surveyed 9 times.
[2]Other perch types identified as: Jo—*Juniperus occidentalis,* Pm—*Pseudotsuga menziesii,* Rp—*Robina pseudoacacia.*
[3]Gravel bars (G) and cliffs (C) were the most used ground perches. G or C designates the perch type most abundant.

TABLE 2. Rankings (highest ranking = 1) of relative abundance of perch types and their use (abundance/use) and the coefficient of rank correlation (r_k) of those rankings for each water body (highest rankings indicated by 1).

Body of water	Ponderosa pine	Snag	Cotton-wood	Man-made structures	Other	Ground[1] G/C	Ice	r_k
Hanford Reach	7/6.5	3/5	4/3	5/4	1/1	G 2/2	6/6.5	.88
Priest Rapids Res.	6/6	4/3.5	2/2	7/6	3/3.5	G 1/1	5/6	.96
Wanapum Res.	6/5	6/5	4/5	3/5	2/3	C 1/1	6/5	.89
Rock Island Res.	5/5.5	2/2.5	1/1	3/2.5	6.5/5.5	C 4/5.5	6.5/5.5	.91
Rocky Reach Res.	2/1.5	4/1.5	1/3	6.5/6.5	3/4.5	C 5/4.5	6.5/6.5	.77
Wells Res.	1/3	4/2	2/1	5/5.5	3/4	G 7/5.5	6/7	.76
Chief Joseph Res.	1/1	2/2	6/4.5	4/6	3/3	C 5/4.5	7/7	.88
Banks Lake	3/4	5/3	4/1	7/7	6/6	C 1/2	2/5	.57
South FDR Res.	1/1	2/2	5/5	6.5/6.5	3/4	C 4/3	6.5/6.5	.96
North FDR Res.	1/1	3/2	5/5	7/6.5	2/4	G 4/3	6/6.5	.88
Spokane R.	1/1	3/2	5/6.5	7/6.5	2/3	C 6/4.5	4/4.5	.88
Pend Oreille	2/3.5	4/2	1/1	3/3.5	5/6.5	G 7/6.5	6/5	.82
Mean	3.0/3.3	3.5/2.7	3.3/3.2	5.3/5.5	3.3/4.0	3.9/3.6	5.6/5.9	
Mean ranking	1/3	4/1	3/2	6/6	2/5	5/4	7/7	

[1]Either gravel bars (G) or cliffs (C), whichever were most abundant (as indicated) were used to rank ground perches.

Several aspects of Bald Eagle perch sites in eastern Washington merit discussion because the perches are either locally valuable to Bald Eagles or subject to impact from human activities, or both. Cliffs provide elevated perches. Lift provided by winds near cliffs allow eagles to fly or soar with a minimal energy expenditure (Stalmaster 1983). Where cliffs were common or abundant a high proportion of eagles were either seen flying or on "ground" perches, primarily cliffs (e.g.; Wanapum Reservoir 69 percent on ground perches, 29 percent flying; Banks Lake 25 percent on ground perches, 25 percent flying, Table 1). Few of man's present activities in eastern Washington affect cliffs used by eagles.

Stalmaster and Newman (1979) found that Bald Eagles preferred perches with an open limb structure allowing good visibility and unobstructed flight. Our eastern Washington studies further support those findings. Ponderosa pine was the most available perch type in eastern Washington, ranking 1 or 2 in abundance along 7 of the 12 water bodies (Table 2). Thirty-four percent of the perched eagles seen during our surveys were in ponderosa pines. Large, old ponderosa pines often have bare limbs and an open limb structure. Snags and many cottonwoods also offer an open limb structure suitable for Bald Eagle perch sites. Cottonwoods and snags were ranked 3 and 4 in mean abundance and accounted for 14 percent and 26 percent of the perched eagle sightings, respectively. Snags seem to be preferred perch sites. Although snags had a mean ranking of 4 in abundance along eastern Washington waters, they had a mean ranking of 1 in use (ranking 3 or higher along 9 of the 12 waters). With the exception of snags, eagle use of perch types correlated (r_k) well with perch abundance along each particular water body (Table 2).

Snags, cottonwoods, and ponderosa pines, and other trees along water bodies in eastern Washington are threatened by many forms of human development (*e.g.,* livestock grazing, logging, firewood cutting, and agricultural, hydroelectric, highway, and residential development). Overgrazing by livestock, often concentrated in riparian areas, can affect recruitment of saplings which would become future perch sites. Logging and firewood cutting removes many large trees and snags which may serve as Bald Eagle perch sites. Clearing shoreline trees for any type of development eliminates potential perches close to the water, the perches which Bald Eagles use most often (Steenhof *et al.* 1980). Vegetation to be inundated by hydroelectric projects in the northwest has usually been cleared as a standard procedure. However, the U.S. Army Corps of Engineers left shoreline vegetation standing as a fish and wildlife mitigation measure when they raised the Chief Joseph Dam and reservoir (U.S. Army 1980). When the water rose, many ponderosa pines drowned and now provide Bald Eagle perch sites as snags. Bald Eagles would benefit should future hydroelectric projects adopt a similar "non-clearing" policy.

Much public land borders the water bodies surveyed in this study. Public agencies should protect present Bald Eagle perch sites and provide for future perches by taking efforts to preserve and perpetuate old growth or large trees along shorelines which they manage. Trees attain larger size than most man-made perches and offer other values (*e.g.,* thermal, visual, wind protection).

Table 1 indicates only slight use of man-made perch sites. However, aerial surveys during previous years, and random sightings indicate frequent use of these structures by Bald Eagles.

Man-made perches, if placed close to water, may increase Bald Eagle use along treeless shorelines. Additional man-made perches would probably be effective along Priest Rapids Reservoir, the lower half of Banks Lake, the lower half of Wanapum Reservoir, and the upper and lower portions of the Hanford Reach because these waters presently lack shoreline perches.

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Diet of Subyearling Chinook Salmon (*Oncorhynchus tshawytscha*) in the Columbia River Estuary and Changes Effected by the 1980 Eruption of Mount St. Helens

Abstract

Stomach contents of subyearling chinook salmon (*Oncorhynchus tshawytscha*) captured in the Columbia River estuary from 1979 to 1982 were examined. Prey were identified and assigned an index of relative importance using percent wet weight and percent frequency of occurrence. Diet was examined to document food resources used at Jones Beach (RKm 75) and to determine if extreme turbidity from the 18 May 1980 eruption of Mount St. Helens caused changes in types of food consumed.

Amphipods, a primary dietary constituent in March, April, and June 1979, diminished in importance following the eruption probably due to heavy siltation. They were almost unused as a food source by subyearling chinook salmon from the eruption in 1980 through 1981. Insects and cladocerans became the primary diet constituents. The taxa and morphological stages of the insects consumed did not change after the eruption.

In 1982, mysids were heavily preyed upon by subyearling chinook salmon. The amphipod population apparently became reestablished, but its importance as a diet constituent was less than that of mysids.

The eruption of Mount St. Helens is not expected to have long term effects on the food resources of subyearling chinook salmon.

Introduction

The eruption of Mount St. Helens on 18 May 1980 altered water quality in the lower Columbia River during the peak migration of subyearling chinook salmon (*Oncorhynchus tshawytscha*) (Dawley *et al.* 1986). Heated mud and ash produced by the eruption flowed from the Toutle River into the Cowlitz River and entered the Columbia River at River Kilometer (RKm) 109 (Figure 1). Turbidity and debris arrived at Jones Beach after sampling was complete on 19 May 1980. Turbidity measurements were made by National Marine Fisheries Service (NMFS) personnel 3 Km downstream from the confluence of the Cowlitz and Columbia Rivers. Decreased feeding rates of juvenile chinook salmon were observed at Jones Beach, Oregon, RKm 75 (Dawley *et al.* 1986); and farther downstream in the Columbia River estuary (McCabe *et al.* 1981); coincident with large quantities of debris and increased turbidity (3000 Jackson Turbidity Units—about 500 times normal). Lowered food consumption could decrease juvenile survival (Snyder 1980) and adversely affect adult returns.

The purpose of this study was to document the diet of subyearling chinook salmon at the upstream extremity of the estuary (RKm 75) and to determine the impact of the eruption of Mount St. Helens on that diet.

The fish were collected as part of a study by the NMFS to define migrational characteristics and survival of juvenile chinook and coho salmon (*O. kisutch*) and steelhead (*Salmo gairdneri*) entering the Columbia River estuary (Dawley *et al.* 1985).

Methods

Fish were collected using beach and purse seines during the spring and summer, 1979-1982. The beach seine was 95 m long and 5 m deep with 1 to 2 cm (stretch measure) webbing (Sims and Johnsen 1974). It was fished from the south shore at RKm 75. The purse seine was 206 m long and 11 m deep with 1 to 2 cm (stretch measure) webbing (Johnsen and Sims 1973). It was fished in mid-river at RKm 75. During May and June, the fishing effort consisted of 10 beach seine and 5 purse seine sets each day beginning at sunrise; during other months, the effort was reduced and varied with the number of migrants being captured. Sampling generally began at sunrise and

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time intervals between sets were 45 min for the beach seine and 90 min for the purse seine.

Captured fish were separated by species; those containing coded wire tags (CWT) (Bergman *et al.* 1968) were sacrificed for tag information. Subyearling chinook salmon predominantly of the fall and summer races (Van Hyning 1973) were separated from yearlings (predominantly of the spring race) by mark information. Stomachs (esophagus to the pyloric caeca) were excised from CWT fish and cleaned of external fatty tissue. Fullness was visually assessed by the proportion of the total stomach length containing food (Terry 1977). A subsample of stomachs containing food was preserved with a buffered 10 percent formaldehyde solution in individual vials for later weight measurements and content analyses. To minimize the effects of digestion on prey identification and to avoid possible bias in our analyses resulting from low counts of prey items from nearly empty stomachs, only stomachs judged half full or greater were selected for content identification.

Organisms were identified to the lowest practical taxon; insects were further separated by metamorphic stage. When dismembered prey were present, parts were weighed together and counts based upon the number of head capsules present. Weight of unidentifiable material was not included in the total weight used for ranking relative importance in the diet.

Stomach contents were examined from 492 subyearling chinook salmon collected from March through June of 1979-1982, and 74 collected from July through September 1980. Data from each year were grouped into 14 d intervals. Comparisons between years were limited to the March-June period.

A modified index of relative importance (IRI') for each taxon present within each 14 d interval was calculated:

$$IRI' = \%W \times \%FO$$

where %W = percent of the total content weight from all stomachs

%FO = percent frequency of occurrence of all salmonids which contain the designated taxon.

The IRI' used was a modification of the multi-variable index, IRI, formulated by Pinkas *et al.* (1971); which included numerical, volumetric, and FO percentages. The modified IRI was used to decrease bias resulting from large numbers of small food items (MacDonald and Green 1983). The IRI' for each taxon is presented as a percentage of the summed IRI''s for all food items.

Results and Discussion

During March-June, 1979-1982, Insecta (54 percent IRI') and Crustacea (41 percent IRI') comprised the major food items found in subyearling chinook salmon (Table 1). The most important order of insects was Diptera, 16 percent IRI'; however, unidentifiable Insecta represented 35 percent IRI'. The most important crustaceans were Amphipoda and Cladocera, which represented 19 and 12 percent IRI', respectively. Mysidacea were important only in 1982 (32 percent IRI'). In July 1980, insects were the most important source of food (62 percent IRI'), but during August and September of that year, Cladocera became the most important constituent of the diet, 94 percent IRI' (Figure 2).

TABLE 1. Percent modified index of relative importance (IRI')[a/] of diet items identified in stomach contents from subyearling chinook salmon captured at Jones Beach, Oregon (RKm 75); March-June, 1979-1982.

Diet item	1979	1980	1981	1982	Average
Insecta					
Unidentifiable	38	33	54	14	35
Diptera	6	12	27	18	16
Misc. Insecta	2	3	4	5	3
Total	46	48	85	37	54
Crustacea					
Amphipoda	40	16	2	17	19
Cladocera	8	25	8	9	12
Mysidacea	2	1	1	32	9
Misc. Crustacea	0	2	1	0	1
Total	50	44	12	58	41
Miscellaneous total	4	8	3	5	5

a/ IRI' = % weight x % frequency of occurrence.

Insecta

Insecta were of major importance in the diet during March-June in all years, particularly in 1981 (85 percent IRI'), when the availability of amphipods appeared to be limited (Table 1).

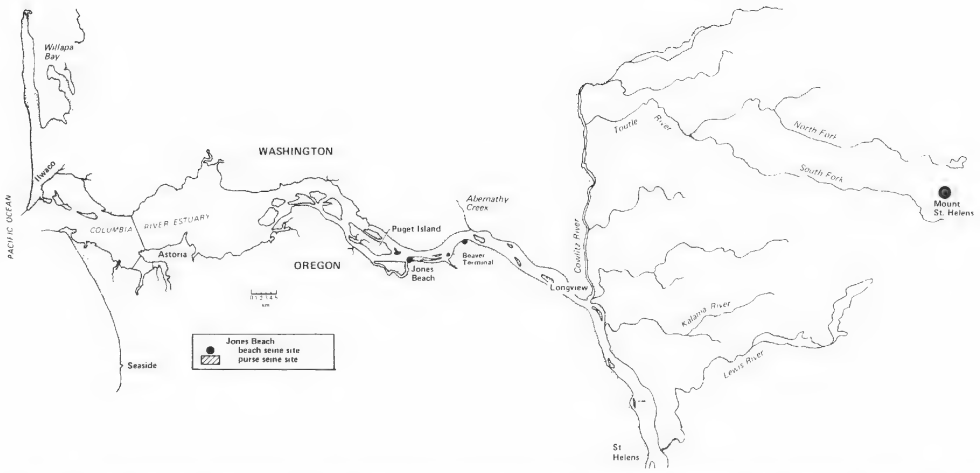

Figure 1. Lower Columbia River showing the Jones Beach sampling site, Cowlitz River, Toutle River and Mount St. Helens.

The types of insects found in the stomachs showed no apparent differences between years, consequently the data for all years were combined by 14 d periods. Diptera were the most numerous insects; 81 percent of 3444 total insects identified to order. There was no seasonal pattern of Diptera consumption for the various metamorphic stages; frequencies of larvae, pupae, and adults were similar. Homoptera and Hymenoptera (mostly adults) were the next most numerous insects—5 percent and 4 percent of the total insects, respectively. Insects representing 10 additional orders were identified; however, each represented less than 3 percent of the total insect count.

Crustacea

The consumption of amphipods varied between years. In 1979, peak consumption of amphipods occurred in late March-early April, 71 percent IRI', followed by a second peak in June, 85 percent IRI' (Figure 2). In 1980, an early April peak at 39 percent IRI' was apparent; however, the June peak observed the previous year was not repeated after the eruption, when the IRI' was only 6 percent. In 1981, minimal amphipod consumption was observed, averaging 3 percent IRI' in March-June. In 1982, amphipods again increased in importance, with peaks in early April

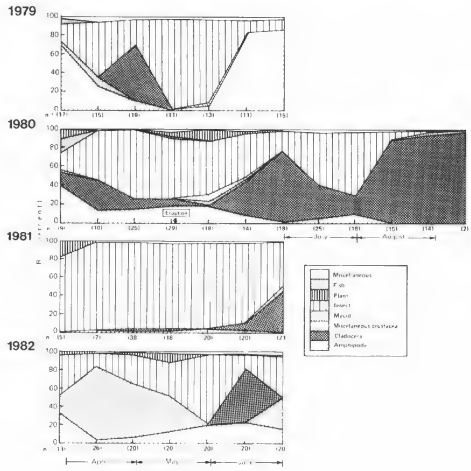

Figure 2. Modified index of relative importance (IRI') for food items consumed by subyearling chinook salmon collected at Jones Beach, Oregon; 1979-1982.

TABLE 2. Amphipod species and percent of total amphipods observed in stomach contents from subyearling chinook salmon before and after the eruption of Mount St. Helens—March-June, 1979-1982.

Species	Before eruption *a/* (%)	After eruption *b/* (%)
Corophium salmonis	74	38
Corophium spinicorne	22	45
Eogammarus confervicolus	4	17

a/ 25 March 1979 to 19 May 1980.
b/ 20 May 1980 to 30 June 1982 (excluding data from July to September 1980).

at 33 percent IRI' and in June at 20 percent IRI'. Meyer *et al.* (1981) observed a similar biomodal peak of amphipod consumption by juvenile chinook salmon in the lower Duwamish River, Washington.

Three species of Amphipoda were found in the stomachs: *Corophium salmonis, C. spinicorne,* and *Eogammarus confervicolus.* Diet compositon after the eruption (Table 2) indicated reduced utilization of *C. salmonis.* Before the eruption *C. salmonis* comprised 74 percent of all amphipods identifiable to species, compared to 38 percent after the eruption. A substantial reduction of *C. salmonis* in the diet of juvenile salmonids following the eruption was also observed in the lower Columbia River estuary by McCabe *et al.* (1981) and Emmett (1982). The greater reduction of *C. salmonis* could be a function of different substrate requirements (Chang and Levings 1976, Albright 1982). Brzezinski and Holton (1981) found that amphipod abundance (primarily *C. salmonis*) was decreased after the eruption in areas of the estuary that had a benthic layer of ash.

In the Columbia River estuary, *C. salmonis* exhibit a bivoltine life cycle (Davis 1978, Wilson 1983). The previous fall generation produces a spring brood in May which matures throughout the summer and subsequently produces a fall brood. The reduction of *C. salmonis* in the diet of subyearling chinook salmon following the eruption suggests that the 1980 spring brood of *C. salmonis* was disrupted by heavy deposition of sediment and that effects continued into 1981 as well.

In March-June, 1979, 1981, and 1982, Cladocera were of major importance in the diet of subyearling chinook salmon (>10 percent IRI') during only one 14 d interval each year (Figure 2). During March-June, 1980, Cladocera were more important (averaging 25 percent IRI'), with a sharp increase following the eruption coincident with decrease consumption of amphipods. In August and September 1980, cladocerans were the major item in the diet. Craddock *et al.* (1976) observed that cladocerans were an important portion of the diet for chinook salmon captured during August-October in the Columbia River at RKm 118.

Mysids (*Neomysis mercedis*) were rare, except in 1982, when they were the dominant food from mid-April to mid-May.

Fluctuations in the abundance of cladocerans and mysids in the diet were apparently unrelated to effects from the eruption (Figure 2). Cladoceran populations are known to exhibit extreme variability in their seasonal and annual abundance (Pennak 1978). *N. mercedis* abundance and distribution have been associated with a number of environmental factors including salinity, temperature, dissolved oxygen, light, and river flow (Hopkins 1958, Heubach 1969, Orsi and Knutson 1979). However, extreme variations in population abundance from one year to the next, unrelated to environmental changes, have been reported (Hopkins 1958, Heubach 1969). It is possible that increased mysid availability in 1982 masked the true extent of amphipod recovery. The decreased consumption of amphipods and increased consumption of insects, mysids, and cladocerans appears to be a temporary change. Partial restoration of amphipod consumption was observed in 1982 and continued improvement of benthic substrate should allow complete recovery to pre-eruption levels. The eruption of Mount St. Helens is not expected to have long term effects on the food resources of subyearling chinook salmon.

Miscellaneous Prey

Fish larvae (Osmeridae) were of minor dietary importance in late March and early April 1979 and 1980, 6 and 15 percent IRI', respectively; none were present in 1981 or 1982.

Immediately following the eruption (20 May-2 June 1980), consumption of plant material increased from 0 to 12 percent IRI'. Relatively high consumption of plant material also occurred 25

March-8 April in 1980 and 1981, 9 and 17 percent respectively, and 6-19 May 1982, 10 percent.

Geographical Differences

From March through June prior to the eruption, subyearling chinook salmon captured at Jones Beach consumed similar proportions of insects and amphipods, whereas upstream from Jonesand amphipods, whereas upstream from Jones Beach in the reservoir of McNary Dam (RKm 470-521) fish consumed insects and cladocerans (R. Fairly, U.S. Fish and Wildlife Serv., Cook, Washington, personal communication) and further upstream in the free flowing Hanford reach (RKm 591-629) fish consumed primarily insects (Becker 1973). Fish captured downstream from Jones Beach (RKm 4-40) consumed primarily amphipods (Durkin *et al.* 1977, 1981).

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Increased Abundance and the Food Consumption of Northern Squawfish (*Ptychocheilus oregonensis*) at River Kilometer 75 in the Columbia River

Abstract

An increase of northern squawfish (*Ptychocheilus oregonensis*) has occurred in the lower Columbia River at Jones Beach, River Kilometer 75, near Woodson, Oregon. A total of 71 squawfish was captured in beach seines from 1966 to 1972 (6650 sets), whereas the average annual catch from 1977 to 1983 was 859 (7602 sets). A sudden increase in squawfish was noted in May 1980 following the eruption of Mount St. Helens. Stomach analysis of squawfish in 1983 indicated that 95 percent contained food, primarily crustaceans, insects, and fish. Juvenile salmon (*Oncorhynchus* spp.) were collected in the same waters, but were not found in the stomachs of any of the northern squawfish examined.

Introduction

For several years the National Marine Fisheries Service has studied the migrational characteristics and survival of juvenile salmonids entering the Columbia River estuary (Dawley *et al.* 1986). The primary sampling site was Jones Beach near Woodson, Oregon, River Kilometer (RKm) 75. Because northern squawfish (*Ptychocheilus oregonensis*) are known predators of juvenile salmon (*Oncorhynchus* spp.) (Ricker 1941, Jeppson and Platts 1959, Thompson 1959, Thompson and Tufts 1967, Steigenberger and Larkin 1974, Uremovich *et al.* 1980, Bentley and Dawley 1981), the numbers of squawfish captured were also monitored.

Northern squawfish captured in beach seines have increased dramatically since 1966 (Table 1). The increasing population of squawfish in the river has a potentially deleterious effect on the survival of juvenile salmonids. This report documents squawfish abundance in beach seine catches at RKm 75 from 1966 to 1972 and from 1977 to 1983. The diets of squawfish captured during July-September 1983 are also discussed.

Methods

A 95 m long beach seine was used that extended out from the Oregon shore to a depth of about 6 m at the outer end of the sweep (Sims and Johnsen 1974). Sampling effort in 1966 and 1967 was limited to 138 and 283 sets, respectively, but during 1968-1972 and 1977-1983 averaged 1237 sets each year (Table 1). Seining generally began at sunrise and continued for seven hours.

A sample of 196 squawfish captured between 20 July and 8 September 1983 were measured to the nearest 0.1 cm (fork length) and immediately immersed in a lethal concentration of ethyl p-aminobenzoate. Because of rapid digestion, as reported by Steigenberger and Larkin (1974), stomach contents were examined within 90 minutes of capture. Food items were separated into four categories: fish, insects, crustaceans, and molluscs. Food categories were evaluated using percent frequency of occurrence, *i.e.,* the portion of the total number of stomachs containing a particular food category. Because our primary concern was salmonids in the diet, the only stomach contents that were precisely identified were fish.

Results and Discussion

The abundance of squawfish at Jones Beach changed dramatically between the two sampling periods. From 1966 through 1972 only 71 squawfish were captured (Table 1). When sampling resumed in 1977, squawfish catches increased substantially; annual catches averaged 401 from 1977 through 1979.

In 1980, the squawfish catch increased to 762, with a sudden increase following the 18 May eruption of Mount St. Helens; 84 percent of the squawfish captured during May were post-eruption and were obtained from 27 percent of the fishing sets. The increased catch continued through July. Beach seine catches of sculpin (*Cottus* spp.), peamouth (*Mylocheilus caurinus*), and sucker (*Catostomus* spp.) also showed dramatic increases following the eruption of Mount St.

TABLE 1. Beach seine catches of northern squawfish in the Columbia River at Jones Beach (RKm 75), 1966-1972 and 1977-1983.

Year	Total	Catch per 100 sets						Total
	Sets[a/]	April	May	June	July	Aug.	Sept.	Catch
1966	138	-[b/]	0.0	0.0	0.0	0.0	0.0	0
1967	283	-	0.0	0.0	0.0	0.0	0.0	0
1968	1,076	0.0	0.0	0.0	0.4	1.0	1.1	4
1969	1,649	0.0	0.4	0.0	0.7	1.7	0.7	10
1970	1,572	0.0	0.5	0.0	0.3	1.1	-	5
1971	999	0.0	0.6	0.8	0.4	0.8	-	6
1972	924	0.0	0.0	0.0	11.4	11.2	-	46
1977	1,400	0.0	0.0	7.8	28.5	101.8	67.9	514
1978	1,171	1.7	0.8	11.7	41.6	57.2	21.1	233
1979	1,211	0.5	4.1	13.9	58.4	94.0	106.2	457
1980	1,136	1.2	19.4/275.0[c/]	47.0	84.4	101.0	78.4	762
1981	1,161	0.5	72.3	252.6	223.9	192.9	159.3	1,754
1982	1,277	4.0	88.5	99.7	204.8	146.9	225.0	1,414
1983	1,266	1.5	69.0	94.8	91.8[d/]	84.2[d/]	58.3[d/]	877

a/ Low catch rates and inconsistent sampling effort between years precluded use of data for the period October-March.
b/ "-" = No effort
c/ Catch before eruption/catch after eruption—139 sets before eruption and 52 sets after the eruption.
d/ About one-half of the fish captured were used for gut content analysis.

Helens. The eruption caused above-average river flows and water temperatures and extreme turbidity in the Columbia River downstream from its confluence with the Cowlitz River (RKm 109). We believe that resident squawfish in the Cowlitz and Columbia Rivers were forced downstream by adverse water quality conditions, resulting in the increased catches.

The peak squawfish catch at Jones Beach occurred in 1981 (1754) and declined in 1982 (1414) and 1983 (877).

Juvenile salmonids were not found in any of the 196 squawfish stomachs examined. However, 14.3 percent of the squawfish examined contained other fishes (Table 2). In the stomachs containing fish, threespine stickleback (*Gasterosteus aculeatus*) were observed in 75 percent, juvenile American shad (*Alosa sapidissima*) in 14 percent, and suckers (*Catostomus* spp.) in 4 percent.

About 95 percent of the stomachs examined contained food items. The most common items were crustaceans (86.2 percent occurrence); insects and molluscs were observed less often (36.2 and 11.7 percent occurrence, respectively). Thompson (1959) and Buchanan *et al.* (1981) observed that squawfish rarely consumed items from more than a single food category; however, 43 percent of the stomachs we examined contained more than one food category.

TABLE 2. Major stomach contents of 196 northern squawfish captured in the Columbia River at Jones Beach (RKm 75), 20 July-8 September 1983.

Food category	No. of stomachs with a certain food item	Frequency of occurrence (%)
Fish (any species)	28	14.3
Stickleback	21	10.7
American shad	4	2.0
Sucker	1	0.5
Unidentified	4	2.0
Crustaceans	169	86.2
Insects	71	36.2
Molluscs	23	11.7

The mean fork length (ML) of squawfish examined was 16.3 cm, with a range of 6.7-45.0 cm (Figure 1). Thompson (1959) found that squawfish of this size were primarily immature specimens, and the diet of immature fish is different than the diet of adults due to their size. Uremovich *et al.* (1980), in a literature review, stated that northern squawfish longer than 15.1 cm fork

length fed occasionally on fish, and those exceeding 30.4 cm fed primarily on fish. At Jones Beach, squawfish longer than 15.1 cm accounted for 65 percent of squawfish examined, and 82 percent of those had fed on fish. Two percent of the squawfish were longer than 30.4 cm, and none contained fish.

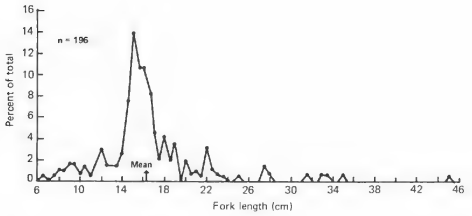

Figure 1. Length frequency of northern squawfish captured in the Columbia River at Jones Beach (RKm 75), 20 July to 8 September 1983.

Squawfish have been described as opportunistic feeders, concentrating on more abundant food sources or those easiest to capture (Thompson 1959, Olney 1975, Buchanan *et al.* 1981). Uremovich *et al.* (1980) sampling in the forebay of Bonneville Dam on the Columbia River, and Bentley and Dawley (1981), sampling in the tailrace of Lower Granite Dam on the Snake River, observed salmonids in 21 percent of the squawfish captured. Thompson (1959) and Thompson and Tufts (1967) reported squawfish predation on juvenile salmon only following releases from a nearby hatchery (2-51 percent occurrence and 1-32 percent occurrence, respectively). Buchanan *et al.* (1981) suggested that previous studies of squawfish predation in flowing rivers were misleading due to the proximity of sampling sites to hatchery release sites or hydroelectric dams where salmon are more vulnerable to predation. During the peak migration period of juvenile salmonids in the free-flowing portion of the lower Willamette River, Buchanan *et al.* (1981) found that only 2 percent of the 1127 squawfish examined had eaten salmonids.

Consistent with Buchanan *et al.* (1981), none of the squawfish we examined contained salmonids even though 8723 subyearling chinook salmon (ML = 8.9 cm, range = 5.0-15.0 cm) were captured coincidentally. We believe that a portion of this salmon population was available to those squawfish larger than 15.1 cm, yet was not consumed. About 6700 juvenile shad (ML = 4.9 cm, range = 3.0-21.0 cm) were also captured but were observed in only 2 percent of the squawfish stomachs. Similar numbers of stickleback (10794) were seined but not measured during this time. They were the most frequently eaten fish species (11 percent occurrence). The varying consumption rates by squawfish for these three fish species may reflect the relative difficulty of capture.

Increased abundance of squawfish at the upstream entrance to the Columbia River estuary has serious implications for salmon managers. Predation by squawfish may be increasing in this area where millions of juvenile salmonids are released each year. In addition, squawfish have been shown to occupy a similar niche and compete with juvenile salmonids for food and space (Jeppson and Platts 1959, Heun 1983).

At Jones Beach, the majority of squawfish captured were juveniles and thus unlikely piscivores; their diet consisted of small crustaceans and insects. The larger adults, which are known piscivores, may also be increasing in other areas of the estuary.

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Announcements

Research News and Comments

From time to time the Editor shall invite a member of the scientific community to summarize current research news of special interest to the readership of *Northwest Science.* The first of these invited articles appears in this issue, and is by Gordon H. Orians of the Institute of Environmental Studies, University of Washington. Orians was chairman of the National Research Council's (NRC) Committee on the Application of Ecological Theory to Environmental Problems. His article summarizes the findings and recommendations of this committee's investigation. My thanks go to Gordon Orians for favoring us with this special piece.

—Editor

Research Grants Awarded by the Northwest Scientific Association

Research grants in the amount of $300 were awarded during 1986 to each of the following students:

Teresa I. Lanier, Dept. Biology, Eastern Washington University
Title: Histologic Analysis of Thyroid Hormone Interactions in the Neural Tissue of *Salmo gairdneri.*

Bryan D. Ness, Dept. Botany, Washington State University
Title: Systematics and Evolution of Subsection Nudi (Calochortus: Liliaceae).

Richard D. Noyes, Dept. Botany, Washington State University
Title: Systematics and Evolution of *Erigeron compositus* (Compositae).

Dawn M. Oen, Pacific University
Title: Systematic Investigations in *Erythronium.*

Paul M. Peterson, Dept. Botany, Washington State University
Title: Genetic Differentiation and Speciation in the *Allium douglasii* Hook Complex (Alliaceae).

Research grants to students will again be offered in 1987. Application forms should be returned to the Chairman of the Research Grants Committee no later than 23 January 1987. For further information and application forms write to:

Dr. George Spomer
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The successful candidates will be announced at the spring meeting of the *Northwest Scientific Association.*

Upcoming Meetings of the Northwest Scientific Association.

The 1987 spring meeting of the NWSA shall be held on the campus of Pacific Lutheran University, Tacoma, Washington 26-28 March. David L. Hansen, Associate Professor of Botany, will be the general program chairman and he will send to each member more specific information.

The 1988 spring meeting of the NWSA is *tentatively* scheduled for March at Southern Oregon State College, Medford, Oregon.

Call for Nominations

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Decline of Second-Growth Douglas-fir in Relation to Great Blue Heron Nesting

Abstract

The effects that great blue herons (*Ardea herodias*) have upon nesting trees, Douglas-fir (*Pseudotsuga menziesii*), were explored in western Washington. An explanation for the decline and death of nesting trees following use by herons is offered. Excrement deposited on the soil beneath nests was analyzed, and found to contain nutrients in amounts beneficial to Douglas-fir. Although soil pH decreased following the onset of nesting, this decrease was not sufficient to adversely change soil nutrient availability. However, heron excrement on needles beneath the nest probably acted as a physical barrier to photosynthetic and to transpirational processes. It was also caustic to needle tissues and resulted in abnormal needle loss. This needle loss was likely the precursor to tree decline.

Introduction

In the Pacific Northwest, great blue herons (*Ardea herodias*) maintain large nesting colonies in the upper branches of Douglas-fir (*Pseudotsuga menziesii*). When walking through an active heron rookery in spring, one is overwhelmed by the smell of excrement and rotting heron food (fish, shellfish and frogs) which cover the forest floor. Those trees that support nests have lost most of their foliage; they appear diseased and near death. The areas directly beneath nesting trees are void of plant growth, in contrast to the lush understory that surrounds the rookery. The association between the presence of heron excrement and the deterioration of nesting trees and their shrub understory, suggests that excrement has caused the observed changes. Dolesh (1984) suggested this type of deterioration was caused by detrimental changes in soil conditions resulting from heron excrement deposits beneath the nesting trees. The objective of this study was to develop a basis for understanding nesting tree decline using (1) a description of the morphological changes that nesting trees undergo, (2) a chemical examination of heron excrement, and (3) an analysis of soil pH beneath nesting trees.

Study Area

This study was conducted on the Washington State Monroe Management Tract located approximately 3 km southeast of the town of Monroe, Washington. An active rookery was the collection site for heron excrement and soil samples, while trees used for crown reconstruction were obtained from within and directly adjacent to a rookery that had been abandoned since 1974.

The stand in which the inhabited rookery was located, was composed of a 60-year-old Douglas-fir and western hemlock (*Tsuga heterophylla*) overstory with sword fern (*Polystichum munitum*) in the understory. It is a relatively flat site (sloping 0-5 percent toward the southeast) at about 180 m in elevation. The stand in which the abandoned rookery was located, was composed of a 100-year-old Douglas-fir and western hemlock overstory along the periphery, with young red alder (*Alnus rubra*) and bigleaf maple (*Acer macrophyllum*) filling in the gaps in the canopy in the center of the rookery. Salmonberry (*Rubus spectabilis*), vine maple (*Acer circinatum*) and sword fern were the dominant understory plants. The site slopes to the northeast (10-20 percent) and is at approximately 230 m in elevation.

Methods

To characterize tree growth responses produced in the presence and absence of nesting, breast height increment cores were removed from trees within and directly adjacent to the abandoned rookery site. From these characterizations, two Douglas-fir, each representing typical growth response patterns expressed in the absence of and following nesting, respectively, were felled for analysis of crown development.

An estimation of the time at which nesting began was necessary to relate nesting activity to periods of tree decline. In order to complete the morphological aspects of this study, the following assumptions were made: (1) Since relatively

large branches are needed to support a heron nest, the second node from the apex bud was assumed to be the highest position or the earliest time that a nest could have been built, and (2) Assuming that herons are responsible for causing malformations typically found in association with heron nests, the year preceding the death of the apical shoot and initiation of compression wood on the lower side of the upturning branch could be considered the latest possible construction time. In this way nest initiation was bracketed to within a few years.

The functional crowns of the sample trees were reconstructed from 1935 until 1980. This was done by counting the number of rings contained within all branches formed after 1934 in relation to the number of annual rings contained within the main stem directly above the point of branch insertion. When a branch becomes nonfunctional, it fails to produce annual rings. The difference between the stem ring count and the branch ring count is the number of years that the branch has been in a nonfunctional state. Functional branches are those branches, generally located in the upper crown, that contribute carbohydrates to the tree stem (Underwood 1967). Changes in this portion of the crown were assumed to represent relevant changes in terms of tree health.

Heron excrement was gathered using three trays (0.6 m x 0.6 m) placed beneath an inhabited tree. The area below the projected crown of the tree was stratified into three horizontal concentric deposition zones, each approximately 0.85 m in width. Each tray was constructed of a corrugated fiberglass base with 2.5-cm fiberglass splash borders, sealed by silicon-based sealer and reinforced by a wooden frame. Inserted in one side of each tray was a garden hose segment that fed into a plastic bag to accommodate rain water. Trays were installed prior to nesting activity in 1982. The contents of each tray was collected and combined at the end of the 1982 nesting season. The excrement was analyzed for nitrogen, phosphorus, potassium, sulfur, calcium, magnesium and sodium content using standard EPA methods (EPA 1979). These values were then expanded from parts per million to grams per square meter.

To assess whether prolonged exposure to heron excrement had altered soil acidity, pH was measured at six depths along five soil profiles beneath nesting trees and five soil profiles beneath trees without nests. Soil pit location was determined randomly where soil was collected from 0, 10, 20, 30, 40 and 50 cm beneath the soil surface. Soil pH was measured in a 1:1 solution using the glass-electrode method (McLean 1982). Analysis of variance was used to evaluate differences in soil pH associated with nesting.

Results

Functional tree crown reconstructions revealed those changes that were associated with nesting. In contrast to the unaffected tree which supported a uniform crown during the 45-year interval, the nesting tree exhibited two periods of crown decline (Fig. 1).

It was estimated that nests were constructed in 1934 and 1958. Within a few years following nest establishment, branch senescence in the lower crown proceeded at an abnormally high rate. Eventually nest level became the upper limit of branch senescence. The tree continued to grow and developed a healthy crown above nest level. When a second nest was established higher in the crown, this nest became the new upper limit of branch senescence (Fig. 1).

Nutrient analysis of the heron excrement revealed that nitrogen and phosphorus were the primary nutrient constituents. Excrement pH was neutral (Table 1).

TABLE 1. Annual nutrient additions and pH of the excrement deposited in trays.

Nutrient	Amount ($g\ m^{-2}yr^{-1}$)
Nitrogen	47.4
Phosphorus	7.1
Sulfur	2.7
Calcium	2.5
Magnesium	0.4
Potassium	0.4
Sodium	0.2
pH	7.0

Soil beneath nesting trees was statistically more acidic than the soil beneath control trees ($P < 0.05$). Soil pH values ranged from slightly above 3.4 to 5.0 (Fig. 2).

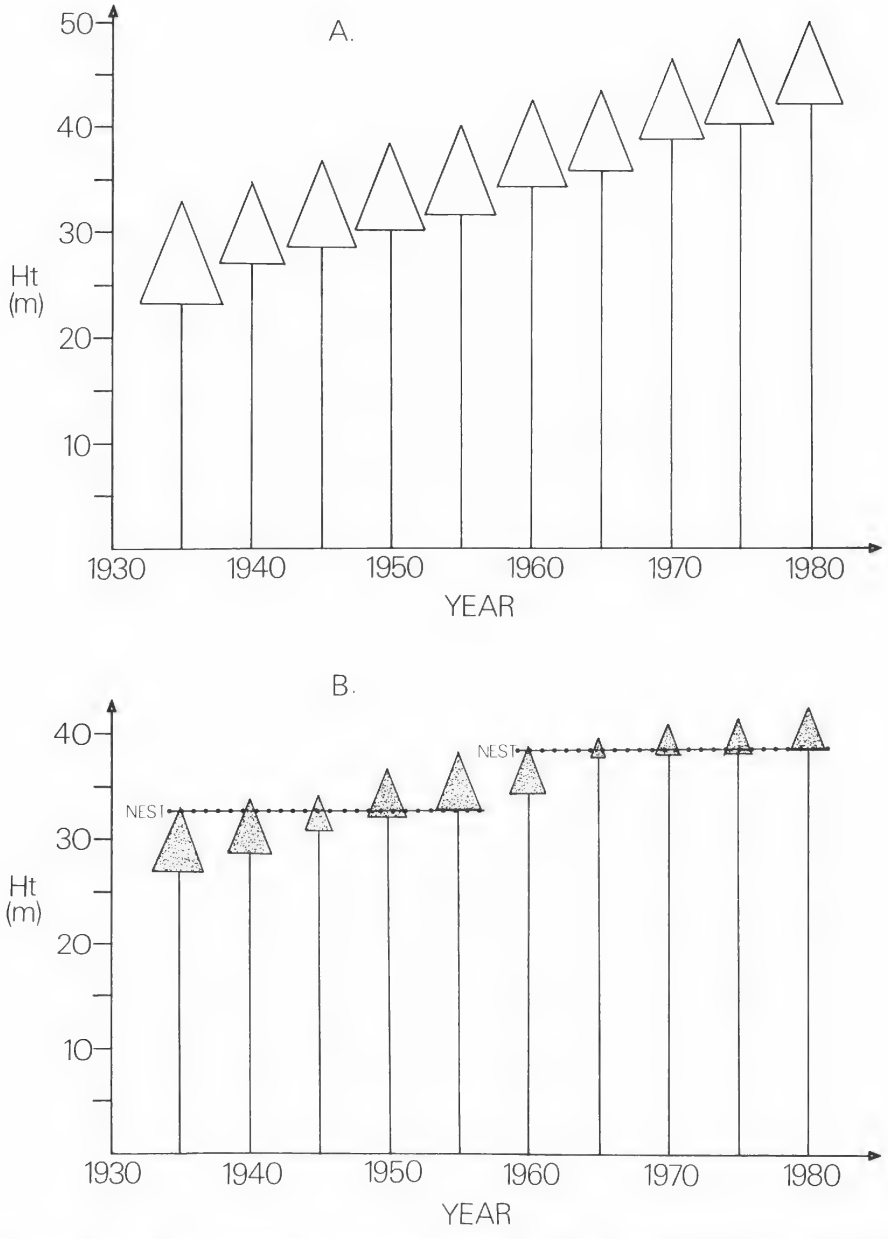

Figure 1. Patterns of crown development for the control tree (A) and the nesting tree (B) at 5-year intervals. Note the relationship between nest height (which remains constant) and the eventual upper limit of branch loss on the nesting tree.

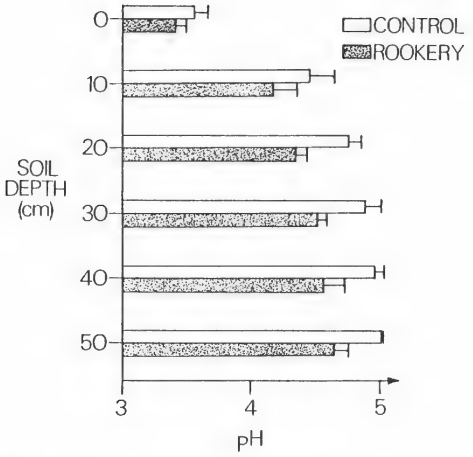

Figure 2. Mean soil pH profiles from beneath nesting trees and from beneath the control trees. The small bars indicate two standard errors of the mean.

Discussion

Tree crown reconstructions showed that within a few years following the establishment of heron nests, branches below each nest died in an ascending direction. The nesting tree exhibited accelerated lower branch senescence following the construction of two heron nests established circa 1934 and 1958. Only those branches in the lower crown were affected; nest level became the upper limit of branch senescence.

Abnormal foliage loss in the lower crown could have been caused by the herons physically debranching the trees while in the process of building their nests. But since herons are relatively awkward when it comes to hovering, it seems unlikely that they would have the opportunity to remove twigs in the lower crown—especially at the branch tips.

Considering the ascending pattern and upper limit of branch senescence, low foliage tolerance to heron excrement is a logical cause for tree decline. Accumulation of heron excrement on foliage would present a physical barrier to essential physiological processes such as photosynthesis, and could also cause chemical burning.

As the grey excrement coats needle surfaces, the amount of sunlight reaching chloroplasts would substantially decrease. The coating would also clog stomata, reducing both carbon dioxide uptake, thus affecting photosynthesis, and water loss, thus affecting transpirational cooling. Impaired photosynthesis resulting from lower effective light levels and restricted carbon dioxide intake, combined with the likelihood of excessive heating, would act to reduce foliage efficiency and longevity.

Another way in which the excrement could affect the foliage is through chemical burning. When concentrated nutrients are applied directly to foliage in aqueous form, osmotic burning has been reported to result (Miller and Young 1976). Concentrations of total nitrogen alone in the heron excrement were within the range of values that have been shown to be extremely detrimental to the foliage of Douglas-fir (Miller and Wert 1979).

The pattern of needle loss sustained by nesting trees shows that needle damage occurs over several years, for the degree to which needles were damaged increased as the time of exposure increased. Branches beneath recently established nests support chlorotic one-year- and two-year-old needles and a few three-year-old needles speckled with necrotic spots. Unaffected trees in the area and the branches above nest level on nesting trees support six age classes of foliage. This evidence suggests these trees have the capacity to tolerate exposure for at least three years. Foliage abscission and the reduction in foliage quality would eventually cause branch death and lead to overall tree decline.

Heron excrement containing concentrated nutrients reaches the soil surface annually. Those nutrients which were contained within these deposits added during a nesting season, were present in concentrations that have been shown to be beneficial to the growth of Douglas-fir (Steinbrenner 1981, Gessell *et al.* 1979, Rustagi and Gupta 1979, B. C. For. Serv. 1971). Nutrients supplied by the herons would supplement existing soil nutrients and should represent a positive influence on tree growth. It is possible that an accumulation of nutrients in the soil or chemicals

not examined in the excrement caused the demise of nesting trees. This possibility, however, is unlikely since only the foliage beneath the nest level was affected. If the foliage loss had been caused by a soil-related factor, such as nutrient toxicity, symptoms of deterioration would be evident throughout the crowns of nesting trees.

The addition of nutrients to soil, particularly nitrogen, has been reported to elicit changes in soil pH (Otchere-Boateng 1979). Changes in soil pH are important since they can drastically affect plant nutrient availability and toxicity. For example, a lowering of pH may make aluminum toxic to roots (Heilman 1981). Extended nest use was associated with a decrease in soil pH beneath nesting trees. The decrease in soil pH however, was still within the range of values that occur in undisturbed Douglas-fir forests (Heilman 1981, Franklin 1970). A lowering of soil pH to these levels is probably not biologically significant. Symptoms of biologically significant changes in soil pH would have been evident throughout the crown and not confined solely to the lower crown.

Conclusions

Great blue heron nesting in Douglas-fir was associated with significant damage to host trees. Since this damage was confined to foliage beneath nests, low foliage tolerance to excrement would appear to be the destructive mechanism involved. Nutrient additions to the soil beneath nesting trees would have probably acted as a positive rather than a negative influence on tree growth.

In a broad sense, damage to nesting trees by herons represents an interesting yet localized problem. In terms of forest dynamics, heron nesting would act to enhance plant diversity through disturbance, where seral trees and shrubs are given space to invade rookery sites. Nesting tree loss would represent a serious problem if availability of suitable great blue heron habitat ever becomes limited.

Acknowledgments

Don Theoe and Lloyd Emery of the Washington State Department of Natural Resources deserve credit for their interest and enthusiasm during the completion of this project. Efforts made by Jacquelyn Erickson and Ray Lee in the field were greatly appreciated. I would also like to thank two anonymous reviewers for their thoughtful suggestions.

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Activity of Little Brown Bats in Coastal Forests

Abstract

Activity of little brown bats was over 75 times greater in lacustrine (lake) habitat than in forest or cutover. Few bats were detected in forest and almost no bats in cutover. Bats were present all night with three peaks of activity in lacustrine habitat. Bat activity was not correlated with insect density.

Introduction

Of the 12 species of bats known from coastal British Columbia, the little brown bat (*Myotis lucifugus*) is the most common and widely distributed. It roosts in trees with cavities or loose bark but readily uses buildings. Roosts provide shelter and protection, and are essential elements in the natural history of temperate bats. Much of the old growth forest containing suitable roosting habitat has been modified by intensive forestry practices. Our objectives were to describe the activity patterns and habitat use of little brown bats in coastal forests. This information would identify habitats important to bats and assist in the development of management plans.

Study Area and Methods

Field work was conducted at the University of British Columbia Research Forest near Maple Ridge, British Columbia. The area contains several small lakes and numerous creeks. Low mountains reach altitudes of up to 1025 m. The study area lies within the Coastal Western Hemlock Biogeoclimatic Zone. Forest harvesting and fires have resulted in a mosaic of seral stages. Although logging has occurred since 1924 in the Research Forest, some stands of conifers older than 100 years still remain. One monitoring site in each of a forest, cutover, and two lacustrine habitats were selected.

Forest: A representative forest stand was selected 2 km south of Loon Lake. The stand was approximately 100 ha, 50 years old and dominated by Douglas-fir (*Pseudotsuga menziesii*), western hemlock (*Tsuga heterophylla*), and western red cedar (*Thuja plicata*). We sampled bat activity from a logging road within the stand.

Cutover: A 30 ha, 2-year old, unburned clearcut was chosen as representative of logged habitat. Dominant vegetation was fireweed (*Epilobium angustifolium*) and hardhack (*Spirea douglasii*). Bat activity was monitored from a logging road that passed through the cutover.

Loon Lake: A 44 ha lake was chosen as representative of lacustrine habitat. Activity was monitored from a small beach. Loon Lake is surrounded by forest with a few small open areas. Log buildings near the lake provided roosting sites for maternity colonies of little brown bats. The largest known colony was in a dormitory 300 m from the monitoring site.

Jacobs Lake: Another small lake (13 ha) was chosen as a second lacustrine habitat. Bat activity was monitored from a short float along the shore. Jacobs Lake was selected because it lacked buildings suitable for maternal roosts and was 2.8 km from Loon Lake. The lake was surrounded by forest similar to that near Loon Lake.

On 23 May 1983, little brown bats were caught in mistnets at Loon Lake and observed at the maternal colony in the dormitory. Bat activity was monitored from 7 June to 20 July using a QMC Mini Bat Detector set for receiving 40 khz signals (Fenton and Bell 1981, Thomas and West 1984). The bat detector was calibrated by releasing little brown bats in a room and setting the detector at the frequency which provided the loudest signal. The bat detector was placed on a tripod or automobile roof 1.5 to 3 m above the ground, heights commonly used by this species (Whitaker *et al.* 1977, Fenton and Bell 1979).

In each habitat, activity was monitored for four nights from 2030 to 0530 PDT. Nights were staggered to ensure a representative sample. Times were recorded when bats passed and ultrasonic signals were detected. Relative activity was measured as the number of bat passes/hour at the various monitoring sites.

Insects were sampled hourly for two nights each in the forest and cutover habitats, four nights at Loon Lake, and for the first two hours of one night at Jacobs Lake. Insects were sampled concurrently with bat activity. Insects were sampled by sweepnetting for 10 minutes near a portable fluorescent lamp. The sweepnet was 43.5 cm in diameter and moved over a 180° arc 1.2 m above the ground at approximately one sweep/sec. Length of the arc and velocity of the sweeps were constant to ensure that the number of insects caught were a measure of relative density. All insects were classified to order.

Results

Bats were active throughout the night at Loon Lake, with three peaks of activity each night (Fig. 1). The first peak of activity, from 2030 to 2230 PDT, was the most intense. A second, smaller peak of activity occurred around midnight, from 2330 to 0130 PDT. A third peak in activity occurred just before daylight, from 0330 to 0530 PDT.

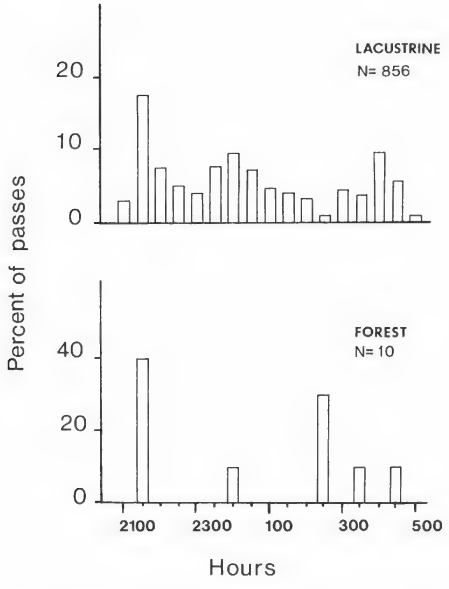

Figure 1. Bat activity in lacustrine and forest habitats. The mean percent activity for Loon Lake was calculated from four nights of monitoring. Percent activity for the forest was based on one night. N is the total number of bat passes recorded.

In the forest, bat activity on 19 June consisted of one pass and on two other nights no bats were detected. Bat activity for 13 June was bimodal and involved 10 passes (Fig. 1). Bat activity within the cutover consisted of a single bat visit during four nights of monitoring. The single pass at the cutover site occurred on 15 July at 2338 PDT.

Bat activity, as measured by the mean number of bat passes/hour, was compared among the three habitats (Table 1). Of the total bat activity, 98.7 percent occurred in the lacustrine habitat. Activity at Loon Lake was significantly greater than in the forest ($t = 6.83$, $p \leq 0.05$) and cutover ($t = 6.91$, $p \leq 0.05$) habitats. Although more bats were detected in the forest than in the cutover, bat activity was not significantly different between these habitats ($t = 1.88$, $p > 0.05$). Bat activity was examined by analysis of variance to determine the importance of time of night and habitat. Although time of night was significant ($F = 2.6$, $p \leq 0.05$), habitat was the most important variable contributing to bat activity ($F = 14.8$, $p \leq 0.05$).

TABLE 1. Bat activity in three coastal habitats.

Habitat	Hours Monitored	Activity ±SE (passes/hour)
cutover	36	0.03 ± 0.03
forest	36	0.30 ± 0.14
lacustrine	36	23.47 ± 3.39

Bat activity at Jacobs Lake was measured to determine if the high activity at Loon Lake was just the result of the proximity of bat roosts in buildings. At Loon Lake (with buildings), there was a mean (±SE) of 32.8 ± 6.9 bat passes/hour in the early evenings. At Jacobs Lake, there was 46.0 ± 20.6 bat passes/hour in the early evening. Bat activity was not significantly different at these lakes ($t = 0.61$, $p > 0.05$).

Flying insects were sampled hourly in each habitat during sampling of bat activity. Diptera comprised 90 to 96 percent of the insects netted next to the fluorescent lamp. The next most abundant order was Lepidoptera which comprised 1 to 9 percent. Relative density of flying insects at Loon Lake was greatest near dusk at about 2130 PDT when 43 percent of the night's insects were sampled. For the rest of night, insect density was relatively low. In the forest, insects were

most abundant at dawn, from 0430 to 0530 PDT, and on average comprised 52 percent of total. Relative insect density in the cutover was greatest at dusk, when on average 87 percent of the total was sampled between 2030 and 2130 PDT.

Relative densities of insects in the cutover and lacustrine habitat were significantly different ($t = 2.76$, $p \leq 0.05$, Table 2). Bat activity was not correlated to relative insect density for the various nights and habitats that were monitored ($R^2 = 0.29$, $p > 0.05$). However, the first peak of bat activity did coincide with the peak on insect activity during the early evening in lacustrine and forest habitats.

TABLE 2. Relative density of flying insects at night in three coastal habitats.

Habitat	Nights Monitored	Total Insects	Mean ±SE (insects/night)
cutover	2	661	330.5 ± 155.5
forest	2	215	107.5 ± 40.5
lacustrine	4	255	63.8 ± 11.6

Discussion

Activity of little brown bats at Loon Lake conformed to patterns reported elsewhere (Kunz 1973, Barclay 1982, Erkert 1982). The middle activity period at Loon Lake may result from female bats returning to the maternity roost to nurse their nonvolant young since it occurs 1.5 to 3 hours after initial emergence (Anthony and Kunz 1977).

Fenton (1970) reports that little brown bats prefer rural areas to forests lacking buildings with roost sites and that lakes are preferred to open fields. Patterns of habitat use in the Research Forest suggest that the affinity of little brown bats to lacustrine habitats is consistent among different geographic regions. The Loon Lake forestry camp had the greatest bat activity measured in the Research Forest.

We do not know if bats using Jacobs Lake were resident or came from Loon Lake. Although little brown bats will travel up to 3 km from their day roost to a feeding site (Anthony *et al.* 1981), their travel time would delay their arrival at Jacobs Lake. Since bat activity at both lakes commenced at about the same time, bats at Jacobs Lake were probably resident in the area. There were no buildings at Jacobs Lake, but bat activity was similar to that at Loon Lake. Hence, the intensities of activity at Loon Lake likely reflect use of lacustrine habitats rather than the presence of buildings for roosts.

Roosts of little brown bats, most common in buildings, also occur in hollow trees or natural crevices with appropriate temperature regimes (Fenton and Barclay 1980). The relatively low bat activity at the forest site may be the consequence of a lack of natural and man-made structures. More likely, bats were roosting in the forest and the few bats detected were travelling to foraging areas in lacustrine habitat. The lack of bat activity in the cutover is consistent with observations reported by Kunz (1973). Clearcutting of forests removes potential roost sites and although insects are abundant the habitat was not used by little brown bats.

Most of the insects sampled in each habitat were species commonly eaten by little brown bats (Anthony and Kunz 1977). Although other studies report that bat activity is directly related to insect abundance (Kunz 1973, Anthony *et al.* 1981, Erkert 1982), no such correlation existed among the habitats we examined. Bat activity was greater in lacustrine habitat than in the forest although insect density was not different. Habitat use may reflect differential foraging success among habitat types.

Lacustrine areas had the greatest amount of bat activity among the habitats we monitored. Because "feeding buzzes" were frequently heard during monitoring of bats at Loon and Jacobs Lakes, lacustrine habitat was used primarily for foraging. Although forests are not heavily used by little brown bats for foraging, they are likely important in providing natural roosts.

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Late-Quaternary Sediments at Battle Ground Lake, Southern Puget Trough, Washington

Abstract

The mineral suites indicate that a major part of the inorganic sediment was introduced to Battle Ground Lake by the wind from sources outside the crater. Basalt derived from the crater itself was reduced to silt and clay by weathering, mixed with eolian sediment, and redeposited in the lake as slope wash. In postglacial time, when soil and forest developed on the crater slopes, the deposition of inorganic sediment, especially the wind-derived component, decreased. Five ash layers are attributed to layers of Sets P, Y, and J of Mount St. Helens and Layer O of Mount Mazama by the proportions of their major minerals:

Layer P, erupted by Mount St. Helens between 2580 and 2930 yr B.P.
Layer Y, erupted by Mount St. Helens between 3350 and 3510 yr B.P.
Layer O, erupted by Mount Mazama between 6700 and 7000 yr B.P.
Layer Ju, erupted by Mount St. Helens at about 10,490 yr B.P.
Layer Jl, erupted by Mount St. Helens at about 11,280 yr B.P.

Introduction

Battle Ground Lake lies in a volcanic crater in the southern Puget Trough of southwestern Washington (Figure 1A). The crater is a closed basin with no inflowing or outflowing streams and a catchment 1.6 times the size of the lake (Figure 1B). Six cores were obtained at different water depths in the lake (Figure 1C) with a 5-cm diameter piston sampler for paleoecologic and stratigraphic studies (Barnosky 1985). Analysis of the pollen and plant macrofossils from the longest cores (Core 80B and 81C) provides a 20,000-year record of vegetation in the unglaciated part of the Puget Trough. During much of the Fraser Glaciation (25,000-10,000 yr B.P.; Waitt and Thorson 1983), the climate was apparently cold and relatively dry (Barnosky 1985). The sudden increase in organic sediments and decrease in magnetic susceptibility (Barnosky 1983, Oldfield *et al.* 1983) suggest that the crater slopes became stabilized as soil developed and temperate trees grew near the lake at the Glacial/Holocene transition.

This paper focuses on the mineralogy and sedimentology of the inorganic sediments at Battle Ground Lake in order to document their distribution. Particular attention is given to identifying the volcanic ash layers which appear in Battle Ground Lake sediments.

Sediment description

A sedimentologic investigation was undertaken on Core 81G in 8.6 m of water at the northeast side of the lake (Figure 1C). This core is similar to cores 80A, 80B and 80C previously described by Barnosky (1985). Two main lithologic units were identified in the core (Figure 2). An upper unit (900-1540 cm below the water surface) consisting of dark gray highly organic gyttja (40 to 80 percent organic matter); the lowest part of this unit (1370-1540 cm) is laminated. A lower unit (1540-1910 cm) consisting of blue-gray clayey silt with little organic matter (ca. 8 percent; Barnosky 1985). Eight thin sand layers, 5 to 40 mm thick, were also present in the core at depths of 1035, 1070, 1355, 1580, 1665, 1745, 1860, and 1870 cm. The crater itself formed through boring lava of early Pleistocene age (Mundorf 1964) and consists of essentially basaltic material (i.e., lava lenses and scoria).

Principal transparent heavy minerals

Seventy-eight samples were taken from core 81G (Figure 2). In addition, two samples of basalt were collected from the crater rim. After crushing, they were given the same treatment as the core samples. Mineralogic analysis was limited to the 63-500 microns fraction due to the difficulty in identifying smaller grains under the microscope. Samples were first washed through screens of 500 and 63 microns. This fraction was dried in the oven at 105°C. One g of each sample was mixed with bromoform in 10 ml centrifuge tubes. The mixture was centrifuged for 1 minute at 4000

rpm. After centrifuging, the bottom of the centrifuge tube was frozen in liquid nitrogen and the supernatant liquid was discarded. After thawing the congealed bromoform, heavy minerals were washed through paper filter with acetone, and mounted on slides in Canada balsam. Two hundred transparent heavy minerals were counted for each sample using the ribbon method (Van Harten 1965).

The relative percentages of the most abundant heavy minerals are shown in Figure 2. Together these minerals constitute about 85 percent of all transparent heavy minerals separated. The other 15 percent predominantly consist of unknown minerals, as well as low percentages of epidote, tourmaline, garnet, zircon, kyanite, titanite, and apatite. The amphiboles (Plate 1A and B) are divided into 5 groups on the basis of their pleochroism: red hornblende (brown to red), basaltic hornblende (yellow or light brown to dark brown), brown hornblende (green to brown), green hornblende (light green to dark green), and cummingtonite (colorless to very pale green). Olivine is colorless, and weathering features were noted along cleavage planes of most of the olivine in the core samples (Plate 1C and D) but not on the olivine from basalt samples collected from the rampart of the crater (Plate 1E and F). A few clinopyroxenes are present. They are light green, generally saw-edged (Plate 1G and H) and are

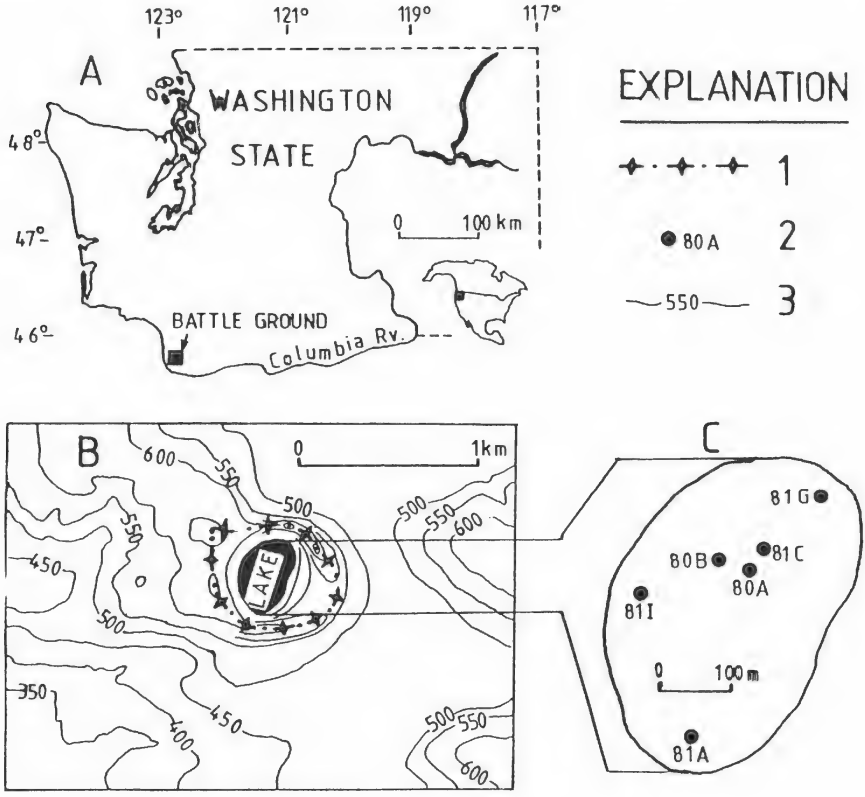

Figure 1.

1.A. Location of Battle Ground Lake, Washington. Lat. 45°45'N., Long. 122°48'W., altitude 155 m.

1.B. Location and shape of Battle Ground volcano.

1.C. Location of the cores (Barnosky 1983).

Abbreviations: 1. Watershed on the volcano. 2. Location of cores. 3. Altitude in feet.

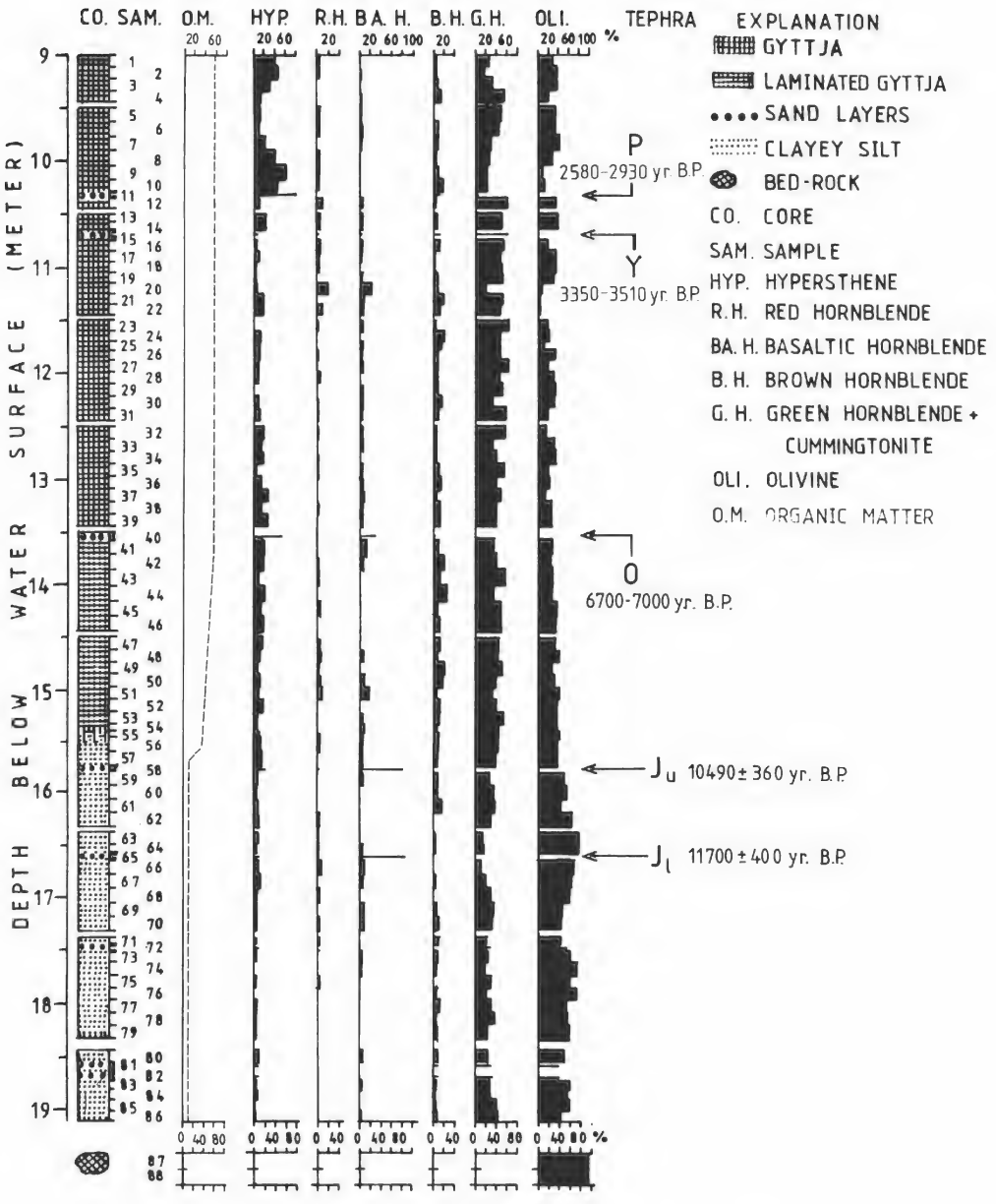

Figure 2. Main lithologic units of Core 81G; location of samples and the most frequent transparent heavy minerals.

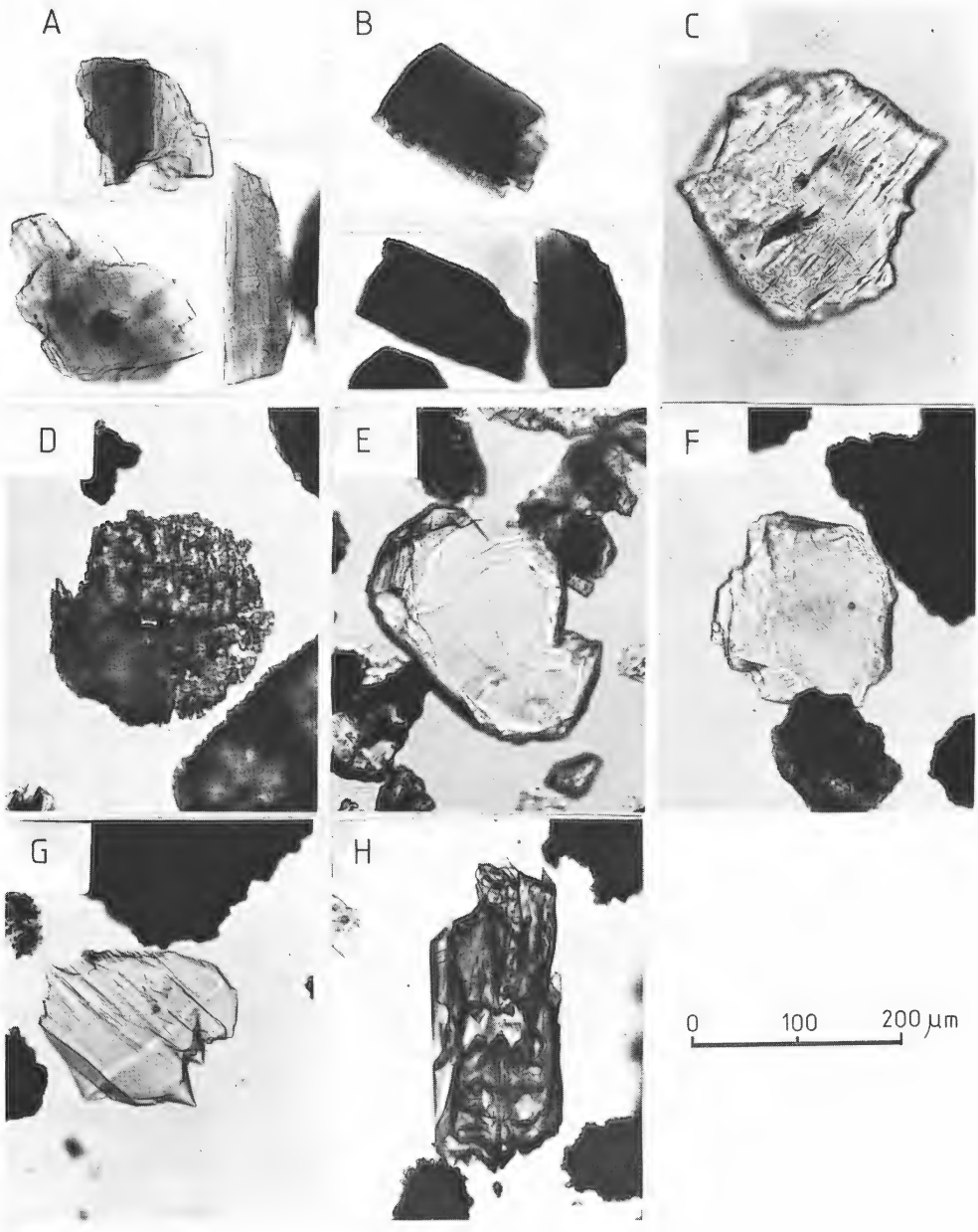

Plate 1
Some minerals from infilling of the lake and from basalt of the rampart:
A, B: amphiboles
C, D: olivine from the infilling
D, F: olivine from samples of basalt of the rampart
G, H: clinopyroxene (augite)

thought to be augite. Aggregates of rutile were found concentrated in samples 59 through 80. They were counted separately from other heavy minerals because they probably formed after sediment deposition. They are up to 15 times more abundant than any other heavy minerals, except in the sand layers 65, 72, 81, and 82.

Provenance of the minerals

The only transparent heavy mineral found in both the basalt and the core samples is olivine. The provenance of all other transparent heavy minerals (including some of the olivine) must be from outside of the crater. Because the crater is a closed depression surrounded by a continuous rampart, wind is considered as the only agent transporting sediment to the lake. This kind of sedimentation was most important in late Pleistocene time, when the vegetation was more open (Barnosky 1985). In Core 81G, this corresponds to the interval from 1540 to 1910 cm.

Barnosky (1984) notes the presence of diatoms indigenous to Tertiary deposits in eastern Washington and in Pleistocene sediments at Battle Ground and suggests that easterly winds may have transported sediments great distances across the periglacial landscape. Wind direction cannot be identified from mineralogical data.

During late Glacial and Holocene time, several ash-falls occurred in the Cascade Range that provided an additional supply of hypersthene and amphibole to the inner slopes of the crater. This explains the overall increase of amphibole and hypersthene, as well as the relative decrease in olivine in the upper unit of Core 81G (Figure 2).

Grain-size of the sediment

Four samples were collected at depths of 1590-1610 cm, 1690-1710 cm, 1790-1810 cm, and 1870-1890 cm. Sand fractions were washed through screens at 1 Phi intervals while silt and clay were treated using the hydrometer-method. The grain-size curves for these samples are very similar as shown in Figure 3A by the shaded area where they overlap. These curves show a modal size at about Phi 6 and a high percentage of silt (about 60 percent falls within the size fraction Phi 4-9) and clay (30 to 37 percent is smaller than Phi 8). The sand fraction, which is very fine-grained, accounts for less than 3 percent of the samples. This grain-size is very different from that of the rampart where boulders, cobbles, and pebbles dominate over a very thin (ca. 10 cm) humic soil. The high content of fine silt and clay can be explained by a mixture of allochtonous eolian sediment and volcanic material from the rampart reduced to silt and clay by weathering before redeposition in the lake through slope wash, wave action, and water currents.

Ash layers

Eight sand layers were analyzed as follows: Color was determined after wet sieving as described above. Heavy mineral content was established by weighing the light and heavy fractions after the separation described earlier. Percentages of transparent heavy mineral suites were calculated on a denominator of 200 grains. Magnetite was identified in each sample but this mineral was not taken into account in heavy mineral suites in order to simplify comparisons with results of previous authors who only referred to transparent mineral suites.

The mineralogy of sand layers 72, 81, and 82 suggests they are not volcanic ash because their minerals are similar to those in samples 66 to 86. On the other hand, sand layers 11, 15, 40, 58, and 65 are allochtonous volcanic ashes. Thickness and grain-size are provided for each volcanic ash layer (Figure 3).

Layer 11: Mount St. Helens Set P
Thickness: 5 to 10 mm.
Color: light gray.
Grain-size: bimodal with 60 percent silt and clay and 40 percent fine and very fine sand at modal size of about Phi 2.3 (Figure 3B).
Composition: most grains of the light fraction are feldspars (approximately 80 percent), the rest are glass and pumice.
Heavy mineral content: 12 percent.
Heavy mineral suite contains: hypersthene, 79 percent; red hornblende, 0.5 percent; basaltic hornblende, 1 percent; brown hornblende 11 percent; green hornblende, 3 percent; unknown, 5.5 percent.

From both stratigraphic position and mineral suite this ash layer is attributed to Mount St. Helens Set P which was previously described by Mullineaux (1974) and dated between 2930 and 2580 yr B.P. (Mullineaux *et al.* 1975).

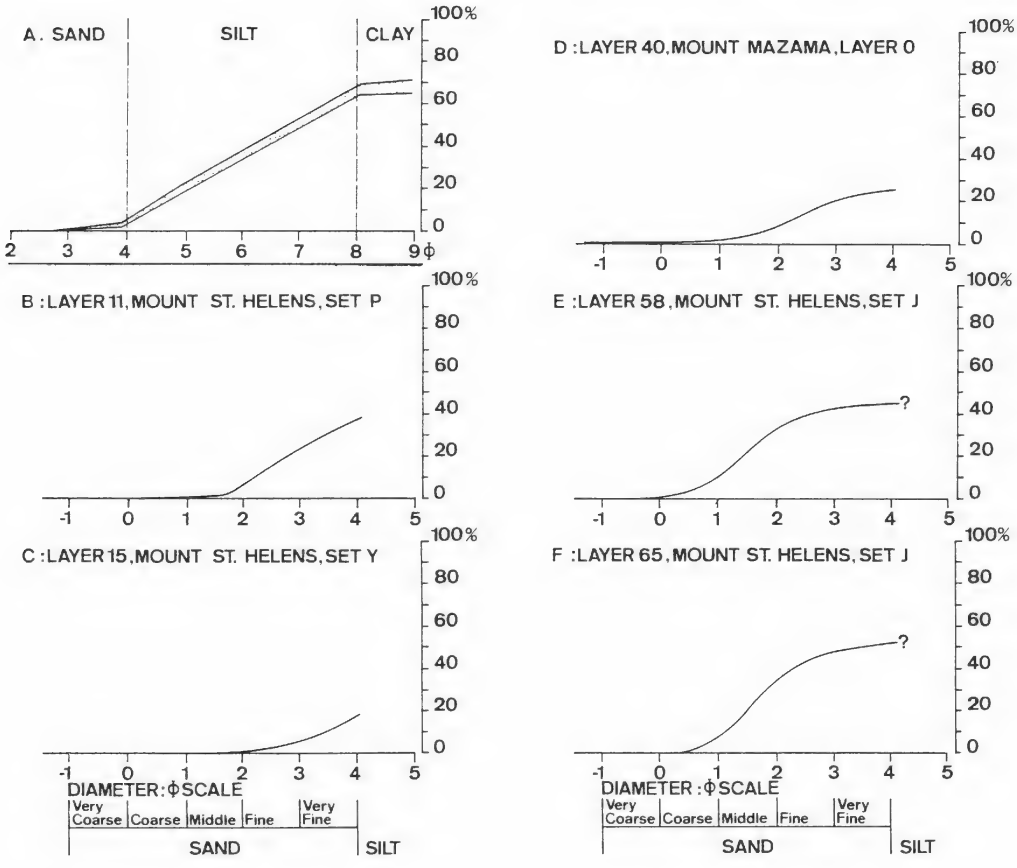

Figure 3

A. Grain-size of four samples collected at depths 15.90-16.10, 16.90-17.10, 17.90-18.10, and 18.70-18.90 m. All curves are included in the shaded area where they overlap. Due to high amount of clay, most of statistical parameters cannot be calculated.

B,C,D,E,F. Grain-size curves of the five volcanic layers of Core 81G. Due to an insufficient amount of fine ash (silt and clay), grain-size analyses were not possible using the hydrometer-method. Hence curves were not drawn beyond Phi 4. Question marks in figures E and F indicate that it was impossible to avoid collecting adjacent gyttja, and an undetermined part of silt and clay is not volcanic material. These curves should be useful in the future to delineate the lobes of each ash-fall as similar data will be provided from other peat-bogs or sections.

Layer 15: Mount St. Helens Set Y
Thickness: 3 to 5 mm
Color: light gray
Grain-size: clay and silt dominate (80 percent) over fine and very fine sand (20 percent) as shown in Figure 3C.
Composition: most grains of the light fraction (80 percent) are feldspars; the rest are glass and pumice.
Heavy mineral content: 8 percent.
Heavy mineral suite contains: hypersthene, 5 percent; red hornblende, 3.5 percent; basaltic hornblende, 2.5 percent; brown hornblende, 11 percent; green hornblende, 43 percent; cummingtonite, 20 percent; unknown, 15 percent.

From both stratigraphic position and mineral suite this ash layer is attributed to an undetermined layer of Mount St. Helens Set Y dated between 3510 and 3350 yr B.P. (Mullineaux *et al.* 1975).

Layer 40: Mount Mazama Layer O
Thickness: 40 mm of graded sediment; the lower 20 mm consists of fine sand and the upper 20 mm consists of silt and clay.
Color: very light gray.
Grain-size: bimodal distribution (Figure 3D) with silt and clay (75 percent) and fine sand (25 percent) at modal size of about Phi 2.3; the coarsest grain is 2.5 mm in diameter.
Composition: most grains of the light fraction are glass and pumice (90 percent); the rest are feldspars.
Heavy mineral suite: hypersthene, 53 percent; red hornblende, 0.5 percent; basaltic hornblende, 30.5 percent; brown hornblende, 4.5 percent; green hornblende, 1 percent; clinopyroxene (augite), 9.5 percent; unknown, 1 percent.

From both its stratigraphic position and mineral suite this layer corresponds to the Mount Mazama Layer O which erupted between 7000 and 6700 yr B.P. (Sarna-Wojcicki *et al.* 1983). The heavy mineral suite can be correlated with those described by Randle *et al.* (1971), Mullineaux (1974) and Juvingné and Porter (1985).

Layer 58: Mount St. Helens Set J
Thickness: less than 3 mm.
Color: light gray.
Grain-size: because the layer is very thin, it was impossible to avoid collecting adjacent gyttja, and an undetermined part of the 55 percent silt and clay is not volcanic material. At least 45 percent consists of middle volcanic sand (Figure 3E) at modal size of about Phi 1.5. The largest grain is 1.5 mm in diameter.
Composition: glass and pumice represent about half of the light fraction and feldspars the other half part.
Heavy mineral content: 13.7 percent.
Heavy mineral suite contains: hypersthene, 17 percent; basaltic hornblende, 81.5 percent; unknown, 1.5 percent.
C^{14} age: a sample of gyttja collected 25 mm above and below the ash layer was dated at 10,490 +/−360 yr B.P. (Lv-1443D).

Layer 65: Mount St. Helens Set J
Thickness: 2 to 4 mm.
Color: light gray.
Grain-size: because the layer is very thin, it was impossible to avoid collecting adjacent gyttja and an undetermined part of the 50 percent silt and clay is not volcanic material. At least 50 percent consists of middle and fine volcanic sand (Figure 3F) at a modal size of about Phi 1.5.
Composition: feldspars (60 percent) dominate over pumice and glass in the light fraction.
Heavy mineral content: 10.4 percent.
Heavy mineral suite: hypersthene, 8.5 percent; red hornblende, 0.5 percent; basaltic hornblende, 88 percent; brown hornblende, 1.5 percent; unknown, 1.5 percent.
C^{14} age: a sample of gyttja collected 25 mm above and below the ash layer was dated at 11,280 +/−590 yr B.P. (Lv-1444D).

Identification of layers 58 and 65

Both layers 58 and 65 are characterized by a high percentage of basaltic hornblende, and a lack of green hornblende and cummingtonite. Mullineaux and Crandell (1981) provide qualitative results for layers J, S, K, and M from Mount St. Helens. Set J is the only one which contains a similar heavy mineral suite as layers 58 and 65. Sets S, K, and M contains about 80 percent amphiboles, most are green hornblende and cummingtonite.

Bracket ages of Mount St. Helens Set J are 8,300 +/−300 and 11,700+/−400 yr B.P. (Mullineaux *et al.* 1975). From both mineralogical

suite and radiocarbon ages, layers 58 and 65 should correspond to Mount St. Helens Set J. Because no precise correlation can be proposed with individual layers of Set J, designations Ju (upper J) for layer 58 and Jl (lower J) for layer 65 are used in Figure 2.

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The Value of Bentonite Mine Spoils in Southeastern Montana as Small Mammal Habitat

Abstract

Bentonite mine spoils in southeastern Montana provided foraging sites for some species of small mammals, but failed to provide cover or burrow sites. Habitat conversions resulting from bentonite mining favored foraging by the pioneering species, deer mice (*Peromyscus maniculatus*) and plains pocket mice (*Perognathus flavescens*), but apparently precluded permanent establishment of any small mammal species. These results indicate the importance of inspecting some study sites for burrows before drawing conclusions on small mammal densities.

Introduction

Bentonite has been surfaced mined in the northern Great Plains for more than 60 years, resulting in the formation of small (less than 5 ha) yet numerous and conspicuous spoil piles from adjacent excavated pits. Bentonite, or the "clay of 1000 uses," is used in a variety of household products (i.e., cosmetics, toothpaste, medicines), is a primary component in oil well drilling mud, and is used in foundry bonding sands (Romo 1981). Because the bulk of the world's supply of sodium bentonite is located in the northern Great Plains (Knechtel and Patterson 1962), it is likely that bentonite mining will remain an important industry is this area.

Bentonite mine spoils have proved difficult to revegetate (Sieg *et al.* 1983). Physical and chemical properties of the spoils materials, sparse and low quality topsoil, low annual precipitation, and livestock grazing hamper natural succession and revegetation efforts. Unreclaimed spoils, even after 30 years, remain steep, barren and sparsely vegetated and early reclamation attempts were only marginally successful (Sieg *et al.* 1983). Studies designed to enhance reclamation success on bentonite mine spoils have been conducted (Bjugstad 1979; Schuman and Seabrook 1984; Uresk and Yamamoto 1986; Voorhees *et al.* 1984), but information pertaining to wildlife use is limited to a study of vesper sparrow (*Pooecetes gramineus*) densities on bentonite mine spoils by Schaid *et al.* (1983). The objectives of our study were to assess the impacts of bentonite mining in southeastern Montana on relative densities of small mammals and to evaluate reclamation attempts in terms of restoring small mammal habitat.

Study Area and Methods

Our study was conducted in southeastern Montana, approximately 9 km west of the town of Alzada. Elevations range from 1000 to 1100 m. The predominant vegetation type (75 percent) on the study area is big sagebrush (*Artemisia tridentata*), with an understory of mainly buffalograss (*Buchloe dactyloides*), and western wheatgrass (*Agropyron smithii*) (MacCracken *et al.* 1983). Scattered bentonite spoil piles and pits constitute approximately 3 percent of the area. The area receives an annual average of 37 cm of precipitation; nearly 50 percent (18 cm) is accumulated between May and July (National Oceanic and Atmospheric Administration 1976). In 1979 and 1980, precipitation during the growing season was 17 percent and 39 percent below normal, respectively.

Twelve 60 x 60-m (0.36-ha) study sites were established: 10 on bentonite mine spoils (ranging in size from 1 to 3 ha) and 2 in adjacent unmined vegetation (Fig. 1). The study sites were classified into 4 site types: 1) old mine spoils, 2) reclaimed spoils, 3) semireclaimed spoils, and 4) sagebrush grasslands. All sites were grazed by domestic livestock.

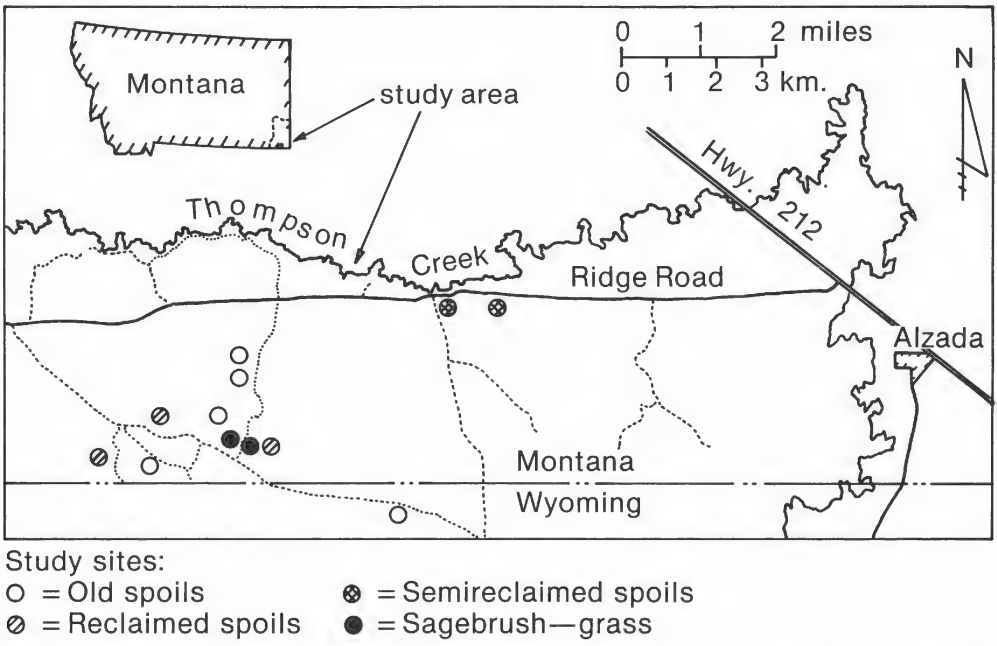

Figure 1. Map of the study area, with regional orientation, showing locations of the 12 study sites near Alzada, Montana.

Five study sites were located on old mine spoils constructed before reclamation was mandated by law. Total plant canopy cover on old spoils averaged 3 percent, and was comprised mostly of rillscale (*Atriplex suckleyi*) and foxtail barley (*Hordeum jubatum*) (Sieg *et al.* 1983). Big sagebrush with an understory of Sandberg bluegrass (*Poa sandbergii*) and green needlegrass (*Stipa viridula*) grew at the base of a north-facing slope on one of the spoils, but was generally absent from other old spoils.

Three study sites were located on reclaimed mine spoils, 5 to 12 years old, which had been recontoured, covered with topsoil, and seeded with a mixture of wheatgrasses (*Agropyron* spp.) and yellow sweetclover (*Melilotus officinalis*). Total plant canopy cover averaged 12 percent and consisted mainly of rillscale and wheatgrasses (Sieg *et al.* 1983). Shrub cover averaged less than one percent, resulting in little vertical structure of the plant community on these sites.

Two study sites were established on semireclaimed bentonite mine spoils that had been recontoured and covered with topsoil the year before our study began. One of the two semireclaimed spoils was seeded with mainly wheatgrasses in the fall of the first year of the study, but the steep grade of the other spoil prevented seeding. Plant canopy cover on the semireclaimed spoils averaged three percent over the 2 years, and consisted mainly of rillscale (Sieg *et al.* 1983).

Two sites were established in gently undulating sagebrush-grass rangeland that had not been disturbed by mining. Total plant canopy cover averaged 32 percent on these sites; big sagebrush constituted 19 percent of the total cover, followed by western wheatgrass (7 percent), green needlegrass, and a diverse mixture of other grasses, forbs, and a few other shrubs.

Small Mammals

To estimate relative abundance of small mammals, on each site 36 Sherman live traps (23 x 9 x 8 cm) were arranged in a grid design with 10-m spacing. Trapping grids on mine spoils were

at least 10 m from unmined vegetation on all sides. Trapping began in April of each year and continued at 3-week intervals until October, except in October 1979, when seeding activities precluded trapping on semireclaimed spoils. Each trapping session consisted of one night of prebaiting following by three consecutive nights of trapping. Traps were opened in late afternoon and checked at dawn the next day. A food supply (rolled oats mixed with peanut butter), along with Dacron batting, was placed in the traps. Upon removal from the traps, animals were first classified by species, then assigned a unique four digit number by toe clipping (Blair 1941). Snap traps were used to collect reference mammals. Small mammal scientific nomenclature follows Hall (1981).

Metal can pitfall traps (15 x 15 cm) were used to sample shrew populations. On each site, 12 cans were buried flush with the soil surface in a grid pattern with 15-m spacing. The pitfall traps were opened every three weeks (during small mammal trapping) from April through October for three consecutive nights by placing a 2- to 4-cm block under the edge of a wooden lid.

Three times during each year, in late spring, midsummer and late summer, the study sites were inspected for small mammal burrows. The number of burrows found along three permanent line transects, 50 m in length and 1 m wide, was recorded for each study site.

Statistical Analyses

One-way analysis of variance and Tukey's multiple comparison procedure (Hull and Nie 1981) were used to compare relative numbers of individual small mammals captured between years and among site types. Bartlett's Box F test was used to test for homogeneity of variances. Data with heterogeneous variances were log transformed. Chi-square contingency tables and Spearman's rank order correlation coefficient (Snedecor and Cochran 1973) were used to compare small mammal composition between years.

Results

Small Mammals

The number of small mammals captured on all study sites was 677 and 347 during 1979 and 1980, respectively. Trap mortality was two percent in 1979 and three percent in 1980. Deer mice were the most abundant mammal, constituting 94 percent of the 1979 captures and 90 percent of the 1980 captures (Table 1). The 49 percent decline ($P < 0.001$) in small mammal captures from 1979 to 1980 was associated with a significant ($P < 0.001$) change in small mammal species composition. Sagebrush voles (*Lagurus curtatus*) were not captured in 1980; however, plains pocket mice (*Perognathus flavescens*) increased ($P = 0.15$) during the second year (Table 1). Dwarf shrews (*Sorex nanus*), masked shrews (*Sorex cinereus*), other shrews (*Sorex* spp.), and thirteen-lined ground squirrels (*Spermophilus tridecemlineatus*) were captured approximately as often in both years.

TABLE 1. Total numbers of small mammals on bentonite mine spoils and sagebrush-grass rangelands in 1979 and 1980, near Alzada, Montana.

Species	*Individuals captured* 1979	1980
Lagurus curtatus	22[a] (3%)[1]	0[b] (0%)[1]
Peromyscus maniculatus	636[a] (94%)	311[b] (90%)
Perognathus flavescens	10[a] (1%)	23[a] (7%)
Sorex spp.	2[a] (1%)	5[a] (1%)
Spermophilus tridecemlineatus	7[a] (1%)	8[a] (2%)
Total	677[a] (100%)	347[b] (100%)

[1]Percent of total capture.

[ab]Numbers in rows followed by same superscript were not significantly different at $\alpha = 0.05$.

Small mammal species richness was low on both mined and unmined habitats. Five species were captured on old bentonite mine spoils; four species were captured on reclaimed and semireclaimed bentonite mine spoils and on sagebrush grasslands (Table 2). Deer mice were the most common species on all study sites. Pocket mouse numbers were low, but similar among mine spoil types, and generally higher on these sites than on sagebrush grasslands. Numbers of thirteen-lined ground squirrels were higher on sagebrush grasslands than on other sites, but ground squirrels were found on mine spoils. Sagebrush voles were captured on all site types, but showed a tendency toward higher

TABLE 2. Two-year average relative abundance (no. individuals/1000 live-trap nights ± SE) of small mammal species captured on bentonite mine spoils and sagebrush grasslands near Alzada, Montana.

Species	----Bentonite mine spoils---- Old	Reclaimed	Semireclaimed	Sagebrush grasslands
Lagurus curtatus	0.8 ± 0.8^{a}	0.2 ± 0.2^{a}	0.4 ± 0.4^{a}	3.8 ± 3.8^{a}
Perognathus flavescens	2.4 ± 0.8^{b}	1.6 ± 1.5^{b}	0.4 ± 0.4^{ab}	0^{a}
Peromyscus maniculatus	39.4 ± 4.7^{a}	62.5 ± 9.4^{b}	29.4 ± 6.4^{a}	41.0 ± 6.3^{ab}
Sorex spp.	0.7 ± 0.7^{a}	0^{a}	0^{a}	1.2 ± 0.1^{a}
Spermophilus tridecemlineatus	0.1 ± 0.1^{a}	0.2 ± 0.2^{a}	0^{a}	2.9 ± 0.2^{b}

^{ab}Numbers in rows followed by same superscript were not significantly different at $\alpha = 0.05$.

TABLE 3. Average relative abundance (no. individuals/1000 trap nights ± SE) of *Peromyscus maniculatus* on bentonite mine spoils and sagebrush-grass rangelands in 1979 and 1980, near Alzada, Montana.

	1979	1980	2-Year $\bar{x}$
Old spoils	52.2 ± 5.7^{a}	26.6 ± 3.9^{ab}	39.4 ± 4.7^{a}
Reclaimed spoils	$90.0 \pm 10.1^{b*}$	35.0 ± 7.6^{b}	62.5 ± 9.4^{b}
Semireclaimed spoils	46.9 ± 8.5^{a}	16.3 ± 6.2^{a}	29.4 ± 6.4^{a}
Sagebrush-grasslands	61.2 ± 5.5^{a}	20.8 ± 4.6^{ab}	41.0 ± 6.3^{ab}

^{ab}Numbers in columns followed by same superscript were not significantly different at $\alpha = 0.05$.
*Different from sagebrush-grasslands at $\alpha = 0.10$.

numbers on sagebrush grasslands. Shrews were limited to sagebrush-grass rangelands and old bentonite mine spoils, but captures were not different ($P > 0.1$) among site types.

The average number of deer mice captured (no./1000 live-trap nights) in 1979 ranged from 52 on old mine spoils to 90 on reclaimed mine spoils; in 1980, captures ranged from 16 (semireclaimed spoils) to 35 (reclaimed spoils) (Table 3). In 1979, deer mouse captures were higher ($P < 0.05$) on reclaimed mine spoils than on all other sites. Relative densities were similar on old spoils, semireclaimed mine spoils, and sagebrush grasslands. However, in 1980, numbers of deer mice were higher ($P < 0.05$) on reclaimed spoils than on semireclaimed spoils, but were similar to captures on old spoils and sagebrush grasslands. Captures were also similar on old and semireclaimed spoils and on sagebrush-grass sites. For the two years combined, captures were higher ($P < 0.05$) on reclaimed bentonite mine spoils than on old spoils and semireclaimed spoils, but were similar to captures on sagebrush grasslands. Average two-year captures of deer mice on old spoils and semireclaimed spoils did not differ significantly ($P > 0.01$).

Burrow Transects

Small mammal burrows were limited to sagebrush-grass rangelands. An average of 50 burrows per hectare were found on the sagebrush-grass sites, whereas small mammal burrows were absent from the bentonite mine spoil habitats.

Discussion

Bentonite mining in southeastern Montana resulted in habitat conversions that generally precluded establishment of small mammal populations, but provided foraging sites for at least deer mice. Although numbers of deer mice were often higher on reclaimed spoils than on other sites, this adaptive rodent was the most common species on all study sites. Deer mice are abundant in a variety of habitats throughout the

United States, and their ability to colonize mine spoils is well documented (e.g. Verts 1959, Kirkland 1976, Steel and Grant 1982). Deer mice were more common on reclaimed coal mine spoils than on unmined sagebrush-grass rangeland in Wyoming, and consumed a variety of plants that grew on mine spoils (Hingtgen and Clark 1984). In our study area, rillscale seeds and bromegrass (*Bromus* sp.) were preferred foods of deer mice captured on the study area (Sieg *et al.* 1986), and the dominance of rillscale in the vegetative cover on the mine spoils likely explained the high use of these sites by deer mice. Greater numbers of deer mouse captures on reclaimed bentonite mine spoils was attributed to higher production of rillscale and slightly greater plant cover on these sites, when compared to old and semi-reclaimed spoils.

Sparsely vegetated mine spoils also provided foraging sites for plains pocket mice. Hispid pocket mice (*Perognathus hispidus*) readily invaded Texas lignite spoils and were captured in low numbers in adjacent abandoned fields (Van-Waggoner 1978). The attraction of plains pocket mice to bentonite mine spoils was attributed to the abundance of rillscale seeds, particularly on reclaimed spoils (Sieg *et al.* In press). However, the absence of sandy soils for both burrowing and dust-bathing (e.g. Kritzman 1974) likely prevented the pocket mice from establishing permanent residency on bentonite spoils.

Sagebrush voles, thirteen-lined ground squirrels, and shrews were associated with sagebrush grasslands. Although captures of sagebrush voles were not significantly higher in sagebrush grasslands than on mine spoils, these voles were captured only in sagebrush communities on north-facing slopes of old bentonite mine spoils, or within 10 m of undisturbed sagebrush grassland on other mine spoils. Sagebrush voles, reported to be among the less common microtines in Montana, are found in close association with big sagebrush (Hoffmann and Pattie 1968).

Two thirteen-lined ground squirrels were captured on bentonite mine spoil habitats: one on the perimeter of an 11-year-old reclaimed spoil, and one in sagebrush habitat on an old spoil. They generally burrow in well-drained soil (Jones *et al.* 1983), and therefore their expansion onto spoils may be limited by their inability to burrow in the spoils material. Further, the near absence of grass cover on the mine spoils may have prevented colonization by ground squirrels inhabitating adjacent sagebrush grasslands. Thirteen-lined ground squirrels were captured in grass, sagebrush, and riparian habitats on our study area and were associated with grass cover among other variables (MacCracken *et al.* 1985b.

Shrews captured on old bentonite mine spoils were within 20 m of native sagebrush-grass vegetation. Litter cover and moist microhabitats associated with dense vegetation have been cited as critical elements in shrew distribution on our study area (MacCracken *et al.* 1985a), and the lack of litter and dense vegetation on the bentonite mine spoils likely explains the general absence of shrews on these sites.

The significant decline in small mammal captures and change in species composition from 1979 to 1980 was attributed to a scarcity of food resources induced by drought. Other authors have attributed changes in small mammal densities (Spevak 1983), species composition (Brown 1973), and restricted breeding activity (Taitt 1981) to food shortages and water stress resulting from annual droughts. In our study, reduced plant canopy cover and aboveground biomass (Sieg *et al.* 1983), as well as lower captures of ground-dwelling macroarthropods (Hull 1981) in 1980 were evidence of diminished food supplies, which undoubtedly influenced small mammal survival.

On mine spoils in Florida (Frohlich and Marion 1984) and in Colorado and New Mexico (Steele and Grant 1982), diverse topography and resulting diverse flora on unreclaimed mine spoils supported a greater number and variety of wildlife species than did reclaimed spoils of relatively uniform topography and vegetative cover. In our study, topographic relief was greater on old (unreclaimed) spoils than on reclaimed sites, but plant species richness, canopy cover, and aboveground biomass were higher on reclaimed spoils than on old spoils (Sieg *et al.* 1983). Further, associated numbers of small mammals were higher on reclaimed bentonite spoils than on old spoils. However, the growth of big sagebrush on steep, north-facing slopes on some old spoils indicates that topographic variations may enhance the growth of some plants, and therefore encourage coloniza-

tion by animals associated with sagebrush grasslands. Therefore, future attempts to reclaim bentonite spoils may be more successful by designing topographic relief into the post-mining landscape.

Successful reclamation of mine spoils for wildlife implies that the reclaimed area provides the basic components necessary for a given species to survive and reproduce. Reclaimed bentonite spoils provided food for at least deer mice (rillscale seeds); however, these sites typically lacked vertical plant structure necessary to provide cover and the spoils materials were apparently impenetrable, based on the absence of small mammal burrows and high penetrometer readings previously reported for these sites (Sieg *et al.* 1983). The value, therefore, of reclaimed bentonite mine spoils as small mammal habitat appears to be as foraging sites. The small size of the spoils results in an "edge effect," which favors pioneer species like the deer mouse. However, in areas where a high percentage of sagebrush grassland is disturbed by numerous bentonite pits, the overall effect on small mammal populations will likely be a decrease in numbers of species such as sagebrush voles, shrews, and thirteen-lined ground squirrels, and a loss of burrow sites for animals adapted to foraging on mine spoil habitats, such as deer mice and pocket mice. Our results also indicate the importance of establishing the presence of burrows before making implications about small mammal population densities on sites adjacent to undisturbed vegetation.

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Post-Glacial Lahars of the Sandy River Basin, Mount Hood, Oregon

Abstract

Within the last 10,000 years, three significant lahar-producing periods have occurred at Mount Hood, Oregon. The Timberline eruptive period occurred between 1400 and 1800 years BP. It was by far the most voluminous of the three periods, producing enough clastic debris to bury the glacial topography of the southwest face of the mountain beneath a smooth debris fan. Smaller debris fans were formed in the upper reaches of the Sandy and Salmon Rivers. Timberline-age lahars traveled the length of the Zigzag and Sandy Rivers, a distance in excess of 90 km. These lahars and associated fluvial deposits helped form flat-floored valleys near the confluence of these rivers and created a delta at the mouth of the Sandy at the Columbia River. The flows probably attained depths of 9 to 12 m above modern river level for most of their passage. Pyroclastic flows of this age traveled at least 13 km from the vent area at Crater Rock along the Zigzag or Little Zigzag Rivers.

Between 400 and 600 years BP, the Zigzag eruptive period produced deposits along the middle reaches of the Zigzag River and the upper Sandy River. Bouldery lahars and fluvial deposits created a terrace 8 to 10 m above present river level along the Zigzag and veneered a Timberline-age terrace on the Sandy River. The Old Maid eruptive period occurred between 180 and 270 years BP. A single lahar flowed down the Sandy River at least as far as Brightwood, 30 km from Crater Rock. Sand deposits that may be related to this event are found down to the mouth of the Sandy River. A single lahar also flowed at least 18 km down the Zigzag River. The lahars, which were probably about 9 m deep, buried mature cedar forests along both rivers.

Introduction

Since the end of the Fraser alpine glaciation about 10,000 years ago, three significant lahar-producing eruptive periods have occurred at Mount Hood. The lahars were confined to river basins originating on the southwest flank of the mountain. The older, Timberline eruptive period occurred 1400 to 1800 years BP (Crandell, 1980), the Zigzag eruptive period 400 to 600 years BP, and the more recent Old Maid eruptive period occurred 180 to 270 years BP (Crandell, 1980). Deposits from the Timberline eruptive period (informally termed Timberline-age in this report) can be traced the length of the Zigzag and Sandy Rivers to the Columbia River. Flows from the Zigzag eruptive period (informally termed Zigzag-age in this report) have been identified only in the middle Zigzag basin and in the upper Sandy basin at Old Maids Flat. Deposits from the Old Maid eruptive period (informally termed Old Maid-age in this report) have been identified from the upper Sandy basin downstream to 2.5 km below the confluence of the Sandy and Salmon Rivers near the hamlet of Brightwood and at a single locality below the confluence of the Zigzag and Little Zigzag Rivers.

Although the lahars from the three eruptive periods affected all drainages on the southwest flank of Mount Hood, this paper will be limited to a discussion of the deposits in the Sandy and Zigzag drainage basins (Figure 1). These basins were chosen due to the concentration of population and recent intense development, which would exacerbate the effects of future eruptions.

Crater Rock

A composite dome known as Crater Rock lies at the apex of the smooth debris fan which gives the southwest side of Mount Hood its distinctive profile (Figure 2). This mass of amphibole-rich phyric dacite sits atop the modern vent, and its extrusion was the probable causative force behind lahar generation.

Field studies and air-photo interpretation show that the Crater Rock dome is composed of at least three lobes (Figure 3). This is based upon degree of alteration, texture, and fabric contrasts between different areas of the dome. The dacite of Lobe 1 has an oxidized, brick red or pink colored matrix, but phenocrysts of plagioclase and amphibole are unaltered. Localized areas of high fumarolic activity have created patches of white and yellow alteration and encrustation. Spires of whitish, pumiceous rock rise 5 to 10 m above the surface of the dome on the north-northwest side of the lobe. The general surface is very irregular and angular with local relief of over 1 m. The lobe shows no obvious fabric.

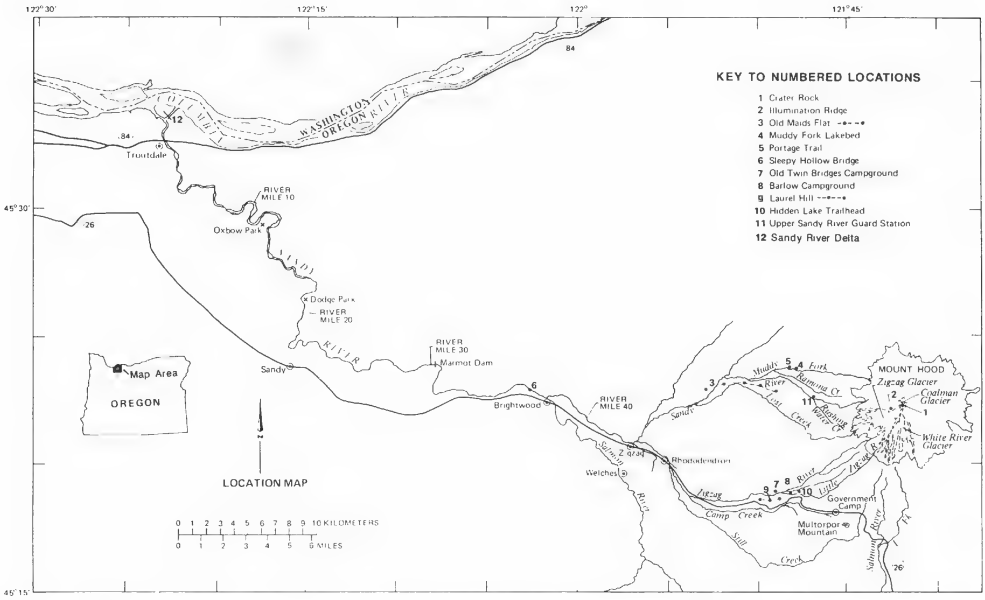

Figure 1. General location map for the Sandy and Zigzag River basins.

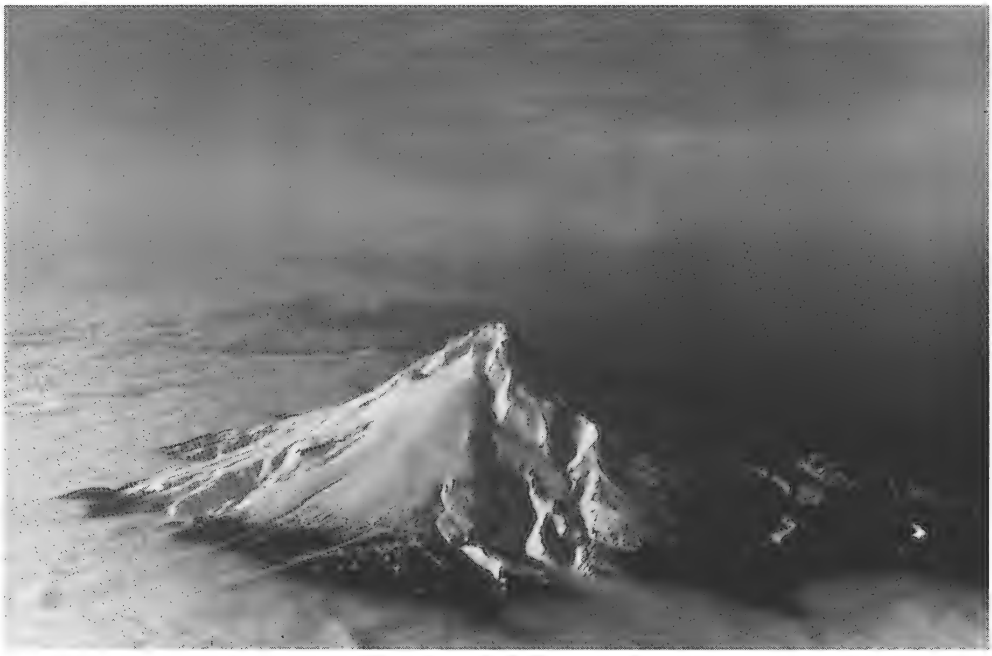

Figure 2. Southwest flank of Mount Hood showing the smooth surface of the main debris fan formed during the Timberline eruptive period, with Crater Rock at its apex. Mount Adams, Washington, is in the background. Photograph by Ellen Cameron.

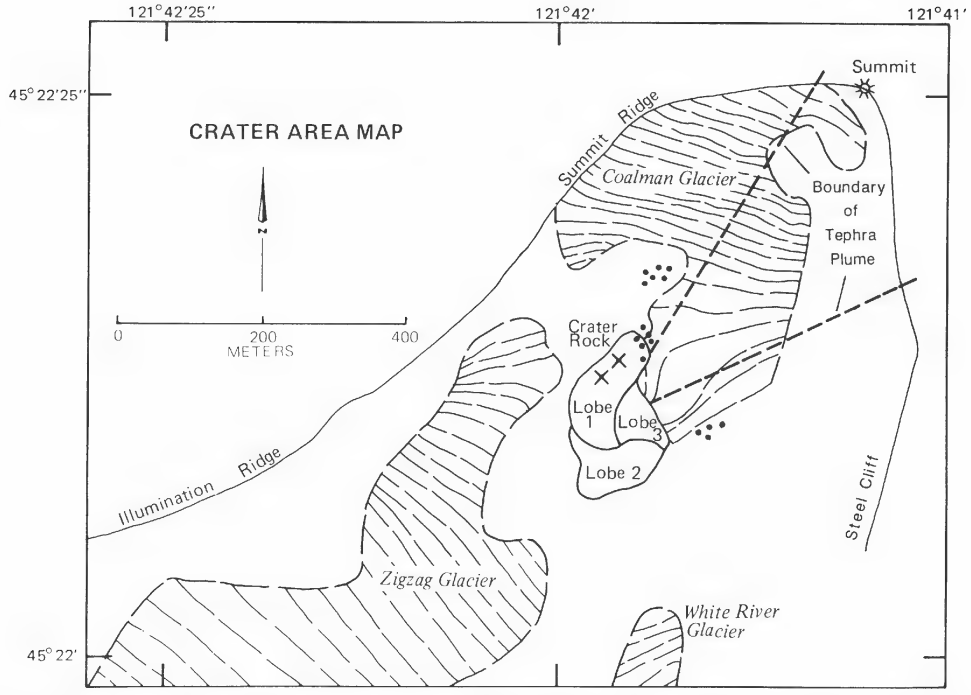

Figure 3. Map view of Crater Rock and surrounding area showing location of the three lobes. Dots represent fumarolic areas. "X" indicates spines on the dome. Dashed lines indicate inferred limits of the breadcrust-bomb tephra plume.

Lobe 2 has an unaltered grey matrix and a much smoother surface texture with local relief of under 1 m. It possesses a general fabric in the form of platy jointing that dips to the southwest (down slope) and is the result of flow within the lobe during extrusion. It is separated locally from Lobe 1 by deep crevasses eroded along the contact. No current fumarolic activity was seen on Lobe 2.

Lobe 3 appears to be the youngest area of the dome. Whether it is a true lobe with extensive talus cover or a deposit of angular clastic debris could not be determined due to snow cover and lack of penetrating exposures. Nevertheless, Lobe 3, as it will be called for convenience, is an area of grey, vesicular, unaltered, angular rubble. Individual clasts average 0.5 m in diameter, but a few range up to 2 m and all sizes commonly show thermally related prismatic fracture patterns. No current fumarolic activity was observed on this lobe.

Two main regions of fumarolic activity flank Crater Rock and bound Coalman Glacier (Figure 3). Temperatures of the fumaroles (84°C to 90°C) are at or below local boiling point. Hydrothermal alteration has reduced the surrounding fragmental debris to sticky yellow, red and blue-grey clay. Both fumarolic areas remain snow-free throughout the winter despite their elevation (3200 m) and prevent Coalman Glacier from joining Zigzag and White River Glaciers.

Timberline Eruptive Period

Timberline-age lahars are the most voluminous of the post-glacial lahar sequences. They form the bulk of the valley-fill deposits in the Sandy and Zigzag basins and the broad fan that extends from Crater Rock to the base of the mountain. Pyroclastic flow deposits of this age have been found as far as Barlow Campground on the Zigzag River (E1/2 NE1/4 Sec 15 T3S R8E), 13 km from the vent area, and lahar and hyper-

concentrated runout deposits as far as the mouth of the Sandy River at the town of Troutdale, 80 km from the source area.

Age and Origin

Radiocarbon dating, of organic debris entrained in the lahars, dates the Timberline flows at 1440 ± 155 to 1780 ± 200 years BP (Table 1). Deposits of Timberline age are found in all drainages on the southwest side of the mountain from the Salmon River (upper reaches only) west to the Sandy River. The extrusion and mass wasting of Crater Rock produced the pyroclastic flows and lahars. Prismatically jointed boulders are common throughout the lower 75 percent of the sequence but rare in the upper 25 percent, suggesting that lahar generation accompanied dome building.

Areal Distribution and General Stratigraphy

The main debris fan (Figure 4) is bounded on the north by Illumination Ridge, on the east by the right lateral moraine of White River Glacier, on the south by Multorpor Mountain and on the southwest by Laurel Hill. The actual thickness of the deposits is unknown, but exposures of over 15 m occur along Highway 26 at Laurel Hill (SE1/4 SW1/4 Sec 14 T3S R8E). Exposures measured from aerial photographs at the headcuts of the Sandy River and Rushing Water Creek are in excess of 100 m in height. These thicknesses probably represent filling of the pre-eruption glacial valleys of the headwaters of these rivers.

Exposures at Laurel Hill (SE1/4 SW1/4 Sec 14 T3S R8E) and in the village of Government Camp next to the fire station (NW1/4 Sec 23 T3S R81/2E), show two discrete textural zones within the Timberline deposits. Matrix-rich, sandy lahars and fluvial deposits constitute approximately the lower one half of both outcrops. Cobble or larger clasts make up less than 10 percent of these flow units. (In all subsequent descriptions of deposits, the term "clast" will be used to mean lithic fragments obviously larger than the matrix material.) Maximum clast size is 10 to 20 cm in diameter. Thinly laminated and cross-bedded fluvial layers up to 10 cm thick intercalate with lahars that average 1.5 to 2 m thick. The sandy deposits of the lower half change abruptly to bouldery lahars and flood deposits of the upper half of the sequence. Here clasts make up 40 to 70 percent of the flow units. Average clast size is 20 to 50 cm in diameter with rare boulders to 2 m. Individual flows are 1 to 1.5 m thick. Lenses of bedded fluvial sand and gravel 20 to 50 cm thick and 1 to 4 m long are occasionally found in the upper half. Weathering of the top unit extends downward for at least 40 cm at all sites measured on the fan, with 40 to 70 cm of weathering typical for deposits of this age in the Sandy River basin (Crandell, 1980).

The timberline-age deposits of the debris fan are veneered by sand- and gravel-sized angular particles of grey, phyric dacite. This is inferred to be air-fall material from small events reported to have occurred in the mid 1800's (Folsom, 1970). This deposit is rarely over 1 cm thick and lies directly on the ground surface.

Below the main debris fan and above Old Maids Flat the Sandy River flows through a narrow gorge cut through the Pliocene volcanic rocks of the Sandy Glacier volcano (Wise, 1969) and the Pleistocene and Holocene deposits of the Mount Hood cone. The high gradient and narrow nature of the gorge precludes the accumulation of more than a trace of deposits.

At the mouth of the canyon, a widening valley and decreasing gradient have allowed the formation of a debris fan at Old Maids Flat which is composed of Timberline-age deposits (Figure 4). The fan, covering an area 0.5 km wide by 1.5 km long, has been dissected by the Sandy River and yields exposures up to 60 m high. The deposits of the Old Maids Flat debris fan show a distinct textural variation similar to that of the main debris fan. The lower one-third is a sequence of sand-rich laharic and fluvial beds ranging in thickness from 1.5 to 3 m, which appear to contain less than 10 percent clasts. The upper two-thirds of the exposure is composed of intercalated cobble and boulder lahars and fluvial beds, with thicknesses ranging from 1.5 to 2 m. Clasts make up 20 to 70 percent of the lahars by volume, the remainder being a matrix of coarse lithic sand. The fluvial beds are generally thinner than the lahars and are composed of stratified sand and gravel. Most of the beds are laterally discontinuous and probably represent fill deposits within shallow, meandering channels on the aggrading fan surface. Cut and fill features are

TABLE 1. Radiocarbon dates from drainages on the southwest flank of Mount Hood.

Location and Setting	Age	Reference
Sandy River near Zigzag, charcoal in duff between lahars SE1/4 SE1/4 Sec 33 T2S R7E	200	Crandell, 1980
White River, terrace near timberline, limb in lahar N1/2 Sec 8 T3S R9E	185 ± 120	Cameron, Pringle
Sandy River, north bank, 2 km NW of Guard Station, Old Maids Flat, charcoal in lahar	220 ± 150	Crandell, 1980
Sandy River, margin of Old Maids Flat, exact location unknown, standing stump buried by lahar	250	Crandell, 1980
White River, upper canyon, standing stump buried by lahar N1/2 Sec 8 T3S R9E	250 ± 150	Lawrence, 1959
White River near Highway 35 crossing, wood in pyroclastic flow SW1/4 Sec 16 T3S R9E	260 ± 160	Crandell, 1980
Zigzag River at Twin Bridges, standing cedar snag killed by lahar NW1/4 Sec 15 T3S R8E	270 ± 150	Cameron, Pringle
White River at Tygh Valley, wood fragments in lahar N1/2 Sec 12 T4S R13E	425 ± 150	Cameron, Pringle
Sandy River at Old Maids Flat, "bayonet tree" buried by lahar NE1/4 Sec 23 T2S R8E	455 ± 135	Cameron, Pringle
Zigzag River near Twin Bridges, standing stump buried by lahar NW1/4 Sec 15 T3S R8E	550 ± 130	Cameron, Pringle
Muddy Fork Sandy River at Portage Trail crossing, Old Maids Flat, wood from ash layer below upper lahar	560 ± 150	Cameron, Pringle
White River at White River Station, charcoal in soil below lahar NW1/4 Sec 30 T4S R10E	1340 ± 160	Cameron, Pringle
Zigzag River at Barlow campground, charcoal from upper pyroclastic flow SE1/4 NE1/4 Sec 15 T3S R8E	1440 ± 155	Cameron, Pringle
Sandy River, south bank, 0.2 km SW of Guard Station, Old Maids Flat, log carried in lahar	1530 ± 200	Crandell, 1980
Near Government Camp, along road, charcoal in ash above glacial age deposits S1/2 Sec 18 T3S R9E	1610 ± 200	Crandell, 1980
Base of Multorpor Mountain, log carried in lahar N1/2 Sec 23 T3S R81/2E	1670 ± 200	Crandell, 1980
White River, top of left lateral moraine charcoal under ash layer NW1/4 SE1/4 Sec 16 T3S R9E	1690 ± 140	Cameron, Pringle
Sandy River near Zig Zag, log carried in lahar SE1/4 SE1/4 Sec 33 T2S R7E	1780 ± 200	Crandell, 1980
White River at Tygh Valley, charcoal in sands below lahar N1/2 Sec 12 T4S R13E	2080 ± 115	Cameron, Pringle
Sandy River 4 km from Brightwood, wood from lahar NE1/4 Sec 22 T2S R6E	40,000	Crandell, 1980

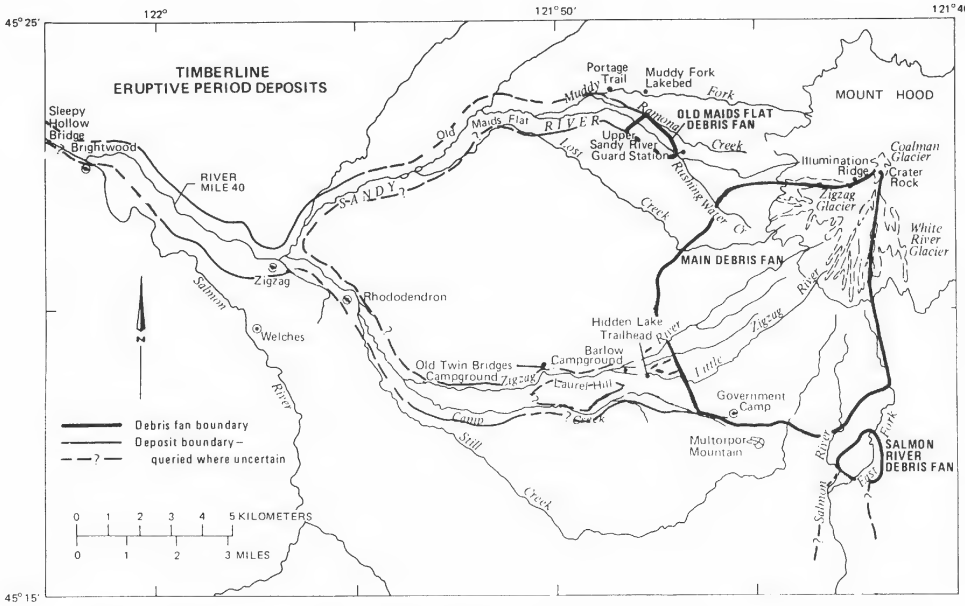

Figure 4. Inundation boundaries of the Timberline eruptive period.

common, with some channels being up to 4 m wide and 2 m deep.

Timberline-age lahars fill the Sandy River valley from the Old Maids Flat debris fan downstream to the power diversion dam at Marmot, forming a flat valley floor 0.5 to 3 km wide. The true thickness of the deposits is unknown, but well-logs from two geothermal test wells located on Old Maids Flat (NE1/4 SE1/4 Sec 15 T2S R8E and SW1/4 SE1/4 Sec 15 T2S R8E) list thicknesses of the mudflow sequence at 80 and 30 m, respectively (Priest and Vogt, 1982).

Exposures 1 to 2 km downstream of the Old Maids Flat debris fan show only the lower, sandy part of the Timberline-age sequence. Individual flows are 1 to 3 m thick and contain less than 10 percent cobble or larger clasts. Maximum clast size is 1 m. Beyond 2 km, only the upper, coarser portion of the sequence is found. The coarser lahars are generally matrix-supported cobble and boulder lahars with clasts composing 20 to 70 percent of the unit. Average clast size is 5 to 10 cm with a maximum of 80 cm. The flows are separated by fluvial sand and gravel. Individual flow deposits average 1 m thick with an observed minimum of 0.4 m and a maximum of 1.2 m. The uppermost unit of each exposure is oxidized to a depth of 40 to 60 cm.

The power diversion dam at Marmot (SE1/4 NE1/4 Sec 13 T2S R5E) marks the transition from valley filling by Timberline-age lahars to migration of the lahars along the river with little deposition. The river flows through narrow, bedrock gorges between river miles 3 and 8, and between 15 and 30. (River miles are marked on most quadrangles for this region and this use is the reason for citing the English measurement rather than the metric equivalent.) Deposits within these reaches are limited to point bars and veneers on lower terraces.

Between the dam and the mouth of the Sandy River Timberline-age deposits were positively identified at only four locations: near the town of Troutdale (NW1/4 Sec 25 T1N R3E), Oxbow Park (SW1/4 Sec 10 T1S R3E), Dodge Park (NE1/4 Sec 36 T1S R4E), and at Marmot dam (NE1/4 Sec 13 T2S R5E) (Figure 1). At each site a maximum of two lahars was found. Average thickness of each lahar deposit was just over 0.5 m with a maximum of 1.5 m at Troutdale. The lahars are generally separated by fluvial or hyperconcentrated runout deposits. Average clast size

is from 2 to 5 cm, with a maximum of 10 cm. All lahar deposits are matrix-supported with clasts composing 30 to 70 percent of the unit.

A well-developed delta occurs at the mouth of the Sandy River which, until the construction of a rockfill dam, split the river into two channels. The surface of the delta is veneered by modern flood deposits from both the Sandy and the Columbia Rivers but it is assumed to be cored by Timberline-age deposits.

As with the Sandy River, the Zigzag and Little Zigzag Rivers pass through narrow, deep canyons in their upper reaches that preclude the accumulation of large deposits. Below the rivers' confluence, Timberline-age lahars have filled the valley to an unknown depth, producing a flat-floored valley extending to the Sandy River valley.

Exposures are rare in the valley below the canyons. The rivers are not actively incising or side cutting, and vegetation extends to the water's edge. A 10 m thick sequence of cobble and boulder lahars is exposed in a road cut at the abandoned bridge over the Little Zigzag River (SW1/4 NW1/4 Sec 14 T3S R8E). These flows came down the Little Zigzag River or spilled over the low saddle divide from the upper Camp Creek area of the main debris fan. Here the lower, sandy portion of the Timberline-age sequence is not present. A quarry near the Hidden Lake trailhead (SE1/4 NE1/4 Sec 15 T3S R8E) exposes at least 8 m of pyroclastic flow and lahar deposits. Two pyroclastic flows are separated by a discontinuous gravel layer and overlie at least one sandy lahar. The upper pyroclastic flow was dated at 1440 ± 155 years BP (Table 1) which places it near the end of the Timberline eruptive period. This exposure is in a 10 to 15 m high terrace formed along a 1 km reach below the confluence of the Little Zigzag and the Zigzag River. It is not known down which river the flows came. The height of the terrace and the thickness of the pyroclastic flow deposits is inconsistent with the lack of downstream deposits. Either erosion has removed the deposits or the flows simply did not extend any farther. A flattening of the valley gradient combined with a constriction in valley width at this point might have caused ponding of the flow.

The only other known Timberline-age deposits found in the Zigzag basin are in shallow exposure of 1 m or less in road cuts and drainage ditches (SW1/4 NE1/4 Sec 16 T3S R8E, road cut; SE1/4 NE1/4 Sec 17 T3S R8E, road cut; NE1/4 SE1/4 Sec 18 T3S R8E, road cut; NE1/4 NE1/4 Sec 19 T3S R8E, drainage ditch).

Timberline-age deposits have been identified only in the upper reaches of the Salmon River, including a well-defined alluvial fan (Figure 4) at the mouth of the upper Salmon River canyon (Sec 19, 20, 29, 30 T3S R9E). Numerous meadows, ponds and bogs occupy a large, low-gradient reach of the river immediately below the fan. No phyric rock types indicative of a Crater Rock origin were found in stream bank deposits in the canyon below the low-gradient reach. Evidently the Timberline-age lahars in the Salmon River were neither voluminous nor energetic enough to cross the low-gradient reach below the alluvial fan.

Physical Characteristics

Timberline-age lahars, exclusive of the debris fans, are generally interbedded with fluvial sands and gravels, this feature becoming more pronounced as distance from the mountain increases. The fluvial interbeds probably represent lahar material reworked by floods that followed shortly after the lahars. Lack of soil horizons between the lahar and fluvial material shows that the time span between the events was minimal. Observations of the lahar deposits of the Toutle River system at Mount St. Helens show that rivers affected by lahars carry large sediment loads until the thalweg has been flushed of sediment. Until then, aggradation of the river bed in low-energy reaches can greatly decrease the carrying capacity of the river channel, making floods more common and severe.

The textural variation of the Timberline-age deposits, with a lower sandy portion and an upper coarser portion, suggest early, fine-grained-producing events and later, coarse clastic material production. The extrusion of the Crater Rock dome might have been preceded by ash emissions and ash-rich pyroclastic flows which, because of the high gradient and available water source in the form of snow and glacier ice, produced the sandy lahars that form the lower portion of the Timberline-age deposits. Once the dome became established, mass wasting or collapse of the growing extrusion would have

supplied the coarse clastics of the upper portions of the sequence.

Clast size generally decreases downstream. Average clast size in the bouldery section of the main debris fan 8 km from the source is 20 to 50 cm in diameter with a maximum of 2 m. On Old Maids Flat, 12 km from the source and downstream from the Old Maids Flat debris fan, the average size is 10 to 20 cm with a maximum of 1 m. Near Brightwood, 40 km from the source, the average clast size is 8 to 15 cm and the maximum is 50 cm. At Troutdale, 80 km from the source, the average size is 1 to 3 cm and the maximum is 10 cm.

Generation of lahars by the extrusion and mass wasting of Crater Rock should have produced a clast lithology predominantly the same as Crater Rock. Samples of average sized clasts were taken from three sites along the Sandy River and the clasts divided into lithologic groups based upon "hand lens" petrology. Sample sites were near Brightwood (SW1/4 NW1/4 Sec 22 T2S R6E, two lahars sampled), Marmot Dam (NW1/4 NE1/4 Sec 13 T2S R5E, one lahar sampled) and Oxbow Park (SW1/4 SW1/4 Sec 10 T1S R4E, one lahar sampled). The sites are 25, 30 and 45 km by river from the source area on the mountain.

Clasts were divided into three dominant rock types: grey-matrix phyric dacite, red-matrix phyric dacite, and "other rocks." Both phyric dacite rock types are similar in gross petrology to lithologic types found on Crater Rock. Phenocrysts comprise 20 to 40 percent of the dacites, with an aphanitic or phaneritic matrix. Phenocrysts are predominantly (80 percent) euhedral plagioclase 1 to 3 mm across with accessory subhedral amphibole 0.5 to 3 mm across. The matrix varies from being truly aphanitic to possessing discernible microlites of plagioclase set in an aphanitic groundmass. Oxidation, which gives a reddish color to some of the clasts, is confined to the aphanitic portions of the matrix with neither microlites nor phenocrysts showing any alteration. At the dome on Mount St. Helens this type of matrix oxidation has at times occurred within months of the extrusion of a lobe. Angular voids less than 1 mm across form up to 5 percent of the volume of some of the clasts.

The "other rock" category includes all rock types other than the phyric dacite. Included are tabular to rounded clasts of aphyric andesite, intrusive rocks from small stocks to the west and southwest of the mountain, and very scoriaceous and altered rocks from lava flows. These "other" clasts are assumed to have been incorporated into the lahar as it moved down stream channels.

Relative percentages among the rock types vary somewhat from site to site, which may be a function of the small sample size (usually 15 to 20 clasts, or all that would fit into an easily carried sample bag). A few trends, however, are distinguishable. Crater Rock-type lithologies generally make up about 60 percent of the clasts by number. This indicates that incorporation of material during flow played an important role in determining the actual volume of the lahar. The rock types represented in the "other rocks" category are found only high on the slopes of the mountain and not from the formations exposed in the valley walls away from the cone, such as olivine basalt of the Sandy River Glacier Volcano, altered basalt of the Miocene Rhododendron Formation, and flows of the Yakima Basalt Subgroup of the Miocene Columbia River Basalt Group. Incorporation of exotic clasts must have occurred primarily high on the cone of the mountain. This premise is supported by personal observations at Mount St. Helens of recent, small scale lahars that showed the lahars to be erosional only in the early stages of flow and to rapidly become depositional.

Estimated Depth of Timberline-age Lahars During Flow

Depth of the lahars during peak flow cannot be determined from the height of deposits above river level, but personal observations of lahars and their deposits at Mount St. Helens provides a basis for some interpretations. On the Toutle River and its North Fork, which resemble the Sandy River below the Old Maids Flat debris fan in channel and valley morphology, the height of the lahar deposits above river level varies between 20 and 70 percent of the true depth of the lahar at peak flow as determined by mudlines and trimlines. In constricted reaches, deposits ranged from 20 to 40 percent of the peak flow height. In more open reaches, deposits ranged from 50 to 70 percent of the peak flow height. In very narrow, steep reaches, such as in the headwaters of the South Fork of the Toutle and in Sheep Canyon, the height of the deposits is less than 1 to 10 percent of the peak flow height.

Deposit height on the Sandy River on Old Maids Flat is 7.3 m above water level; at the confluence with the Zigzag River, 8.5 m; at Sleepy Hollow bridge, 8.5 m; at Oxbow Park, 7.0 m; and at Troutdale, 5.8 m. All of these sites are in open reaches; therefore, it can be conservatively estimated that peak flow heights of the lahars approached one and a half times the height of the deposits. This would produce a peak stage 9 m above the present river level at Troutdale and 10 to 12 m at the upstream sites.

Zigzag Eruptive Period

Deposits from a previously undescribed sequence of lahars and associated fluvial deposits form an 8 m high terrace along a single reach of the Zigzag River just below its confluence with the Little Zigzag River (Figure 5) and caps part of a 30 m high erosional terrace in the Old Maid debris fan. This sequence has the lowest volume and extent of the three major post-glacial lahar sequences. Within this paper it will be referred to as the Zigzag eruptive period.

Age and Origin

Along the Zigzag River (N1/2 Sec 15 T3S R8E) the flows buried a stream-bank forest of mature Douglas fir, and standing trunks still exist that are at least 2 m tall. The bark from one of these stumps has been dated at 550± 130 years BP (Table 1). This date corresponds well with the 560 ± 150 years BP age of wood from a tephra layer in the upper Sandy River basin and suggests an eruption which produced both lahars and air fall material. On the Old Maid debris fan 1 km downstream from the Upper Sandy River Guard Station (NE1/4 Sec 23 T2S R8E) a single sandy, cobble lahar caps an erosional terrace 30 m above present river level. The flow overran and charred a stand of young Douglas fir trees 5 to 10 cm in diameter. These trees are aligned in downstream orientations similar to the "bayonet" trees flattened by the lahars at Mount St. Helens (Janda and others, 1980). Wood from these trees has been dated at 455 ± 135 years BP.

Areal Extent and Stratigraphy

Laharic deposits of this age are restricted to a terrace on the right bank of the Zigzag River below its confluence with the Little Zigzag River and veneer a terrace in the Timberline-age deposits of the Old Maid debris fan (Figure 5). The Zigzag basin terrace is at least 1 km long and averages 100 m wide. It merges with the valley wall at its upstream end and terminates abruptly downstream in a series of erosional terraces. The valley narrows considerably at this point and may have caused ponding of the flows, creating the thick, localized deposits and may explain the lack of any exposures downstream. It is in this reach that the thick but not laterally extensive Timberline-age pyroclastic flows are found. They, too, may have ponded behind this valley constriction.

The terrace is composed of a lower, bouldery deposit 3 to 4 m thick that is massive and made up of rounded clasts up to 0.5 m in diameter set in a sandy matrix. Portions of the deposit are clast-supported. The flows engulfed a forest of mature Douglas fir trees up to 0.5 m in diameter but left the bark intact on the upstream sides and undamaged brushy branches wrapped around the trunks. The rooted bases of some of these stumps are at the modern river level and show that the Zigzag River has returned to the base level which existed before the formation of the terrace.

Overlying the bouldery deposit are 2 to 3 m of intercalated lahar, hyperconcentrated runout and fluvial sand deposits. These units are generally less than 1 m thick and are not laterally traceable. They represent thin flows which washed over the flat surface of the fill material immediately after its emplacement. The thin units are topped by 10 cm of soil and forest duff which is in turn overlain by a lahar of Old Maid-age.

The deposit on the Old Maid debris fan terrace is 0.9 m thick and represents a single, sandy cobble lahar. The height of the terrace above river level at the time of the lahar is unknown, but it is 30 m above modern levels. The deposit now supports a Douglas fir forest of greater density and size than elsewhere on the Old Maids Flat surface. This vegetative difference is readily apparent on air photos and shows that the deposit is limited to a terrace 0.5 km long and 100 m wide. No other evidence of this flow is found in the Sandy basin.

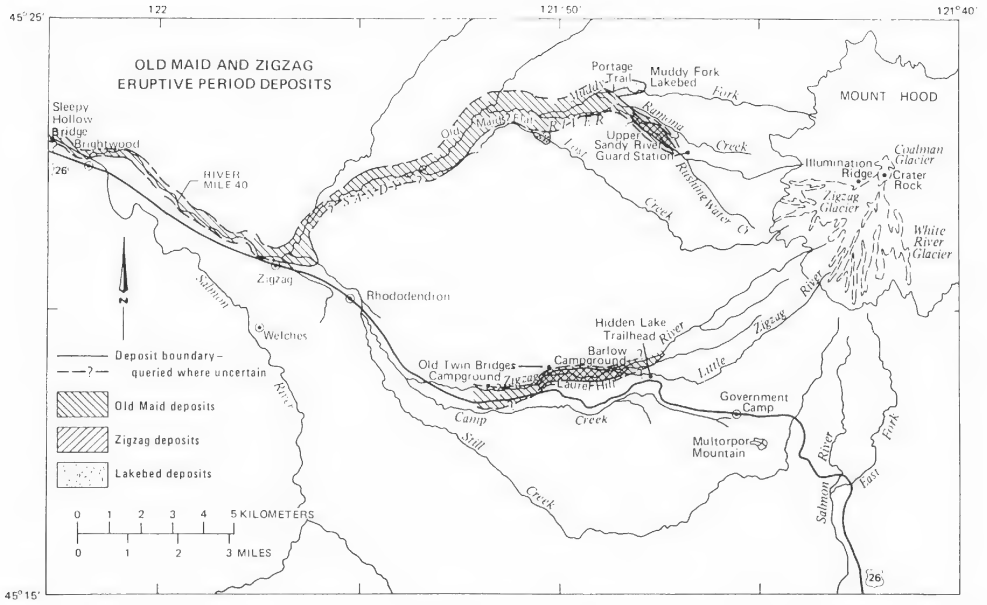

Figure 5. Inundation boundaries of the Zigzag and Old Maid eruptive periods and the location of two Old Maid age lakes.

Old Maid Eruptive Period

More than 20 exposures of Old Maid age lahar deposits have been located in the Sandy and Zigzag River drainages. Although a succession of Old Maid age lahars is found in the White River canyon on the south side of Mount Hood, only a single lahar unit has been identified in the Sandy and Zigzag basins in any one exposure. Old Maid age deposits essentially form a veneer on the surface of the voluminous Timberline-age deposits and on the Zigzag-age deposits along the Zigzag River (Figure 5). No deposits of Old Maid age were identified in the Little Zigzag and Salmon Rivers or in Still and Camp Creeks.

Age and Origin

Radiocarbon dating of wood samples suggests that the Old Maid eruptive period occurred between 200 and 300 years BP (Table 1). Historical accounts and dendrochronological work extend the lower limit to about 180 years BP.

In November of 1805 and April of 1806, Lewis and Clark explored a river they named Quicksand River. Captain Clark described it as follows in his journal (Thwaites, 1959), reproduced here with original spellings:

"... I arrived at the enterence of a river which appeared to scatter over a Sand bar, the bottom of which I could see quit across and did not appear to be 4 Inches deep in any part; I attempted to wade this Stream and to my astonishment found the bottom a quick Sand, and impassable ... this river which we found to be a verry considerable Stream Discharging its waters through 2 chanels which forms an Island of about 3 miles in length on the river and 1 1/2 miles wide, composed of corse sand which is thrown out of this quick sand river compressing the waters of the Columbia and throwing the whole current of its waters against its Northern banks ... This stream has much the appearance of the River Platt, roleing its quick sands into the bottoms with great velocity after which it is divided into 2 chanels by a large sand bar before mentioned, the narrowest part of this River is 120 yards." (3 Nov. 1805) "... above the point which it divided itself into two chanels, it is about 300 yards wide tho' the chanel is not more than 50 yards, and only 6 feet deep. the other part of the river from 2 to 4 inches water, the bead of this river is formed entirely of quick sand; its banks are low and at present overflown. the water is turbed and current rapid." (1 April 1806)

The name of this river was shortened in later years to the Sandy River. The Sandy River is now

a boulder-armored river and the channel immediately above the delta is at least 3 to 4 m deep. Modern fall and spring floods do not generally overtop its banks. The expedition appears to have arrived while the river was still flushing the sediment of the Old Maid event through the system. Taking into account the rapidity with which some of the streams surrounding Mount St. Helens have recovered from damage induced by the 1980 eruption (staff members of the Cascades Volcano Observatory, personal communications, 1984), it is possible that the Lewis and Clark Expedition arrived within 5 to 10 years after a laharic event.

Dendrochronologic samples were taken in the vicinity of Old Maids Flat in an attempt to refine the age range established by radiocarbon analysis and suggested by historical accounts. At Mount St. Helens, trees at the periphery of the May 18, 1980 mudflows commonly had large patches of bark removed on their upstream sides by abrasion but managed to survive. It is assumed that damage of this magnitude would affect the growth rate of the tree and cause an abrupt narrowing of the annual rings.

About 20 old growth fir and cedar trees were cored around the edges of Old Maids Flat. Several trees near the confluence of the Muddy Fork and the Sandy River show a consistent narrowing of rings between 1760 A.D. and 1805 A.D. with a possible drastic thin sequence starting about 1794 A.D. and lasting for an average of 10 years. The ensuing rings also show the presence of traumatic resin canals, which have been associated with the recovery response of a tree to physical injury. Trees higher on the hillslopes do not show the narrowing or the concentration of resin canals. These preliminary findings suggest that a tree-damaging event, possibly a lahar, occurred around the year 1794 A.D. The narrow rings starting in 1760 A.D. may indicate the beginning of ash falls in the basin which slowed the growth rate of the trees. Ring counts in 1984 on stumps rooted in the Old Maid-age surface show maximum ages of 173 years in the Sandy basin and 190 years in the Zigzag basin, or 1811 A.D. and 1794 A.D., respectively.

The formation of lobe 3 of Crater Rock is a possible method of generation for the Old Maid lahars. The very angular nature of the lobe material and its complete lack of oxidation and weathering provide evidence for a recent origin. The close proximity of the lobe to Coalman Glacier (Figure 3) and the normal snowpack expected at this elevation would provide the water needed for lahar generation through melting of the snow and glacial ice.

A deposit of grey tephra mantles the normally light colored material of the summit ridge. From its shape, the deposit had its origin at Crater Rock. The tephra has a maximum observed thickness of 20 cm at the summit and exhibits some stratification that may be due to reworking by wind. Breadcrust bombs are common throughout the deposit, averaging 15 cm across but with occasional bombs up to 0.8 m. The actual age of this ash is not known, but the fact that the loose ash is still quite visible in a very windy location and that the highly fractured surfaces of the breadcrust bombs are sharp and unaltered by the freeze-thaw cycle requires a relatively young age. The Old Maid eruptive period is the last of the major eruptions at Mount Hood; the ash and bomb deposit may be contemporaneous with it.

Areal Distribution

The highest irrefutable exposure of Old Maid age deposits in the Sandy River basin was found about two km downstream from the Upper Sandy Guard Station. At this point the lahar ceased being channelized and began overbank deposition across most of the surface of Old Maids Flat. A possible Old Maid age deposit is found in the very high-gradient upper and middle reaches of Rushing Water Creek. This grey, sandy deposit is found in patches along low ridge crests and terraces.

In the Old Maids Flat area, the Old Maid age lahar forms a veneer from 0.2 to 1 m thick on pre-existing terraces and over most of the surface of the Flat. Most of the exposed sections range between 0.5 and 0.8 m thick. Deposits up to 3 m thick are found along the stream channel of the Muddy Fork of the Sandy River downstream from the Portage Trail crossing (E1/2 Sec 15 T2S R8E). The pre-lahar channels of the Muddy Fork and Ramona Creek were incised into the Timberline age surface of the Flat and lined with old growth cedar trees up to 2 m in diameter. The Old Maid age lahar filled these channels and adjacent low areas, killing the trees. Their remains are still apparent in the form of tree wells

and standing snags up to 30 m tall. Inferred depths of the pre-lahar channels of 1.6 to 6.5 m were obtained by sounding tree wells and the interiors of hollow snags.

None of the exposures of the Old Maid age lahar within the Sandy River drainage provides evidence of multiple flows. Apparent stratification in a deposit forming the north bank of Muddy Fork 100 m downstream from the crossing of the Portage Trail may reflect individual surges of pulses as a single flow spilled into and flowed down the old channel. A thin (2 to 6 cm) layer of moderately well sorted sands, possibly the sole or basal layer (Kevin Scott, personal communication, 1983), underlies the above unit.

At least one and possibly two temporary lakes were formed along the margins of Old Maids Flat through damming of tributaries by the Old Maid age lahar (Figure 5). The largest and best defined of the temporary lakes formed at the mouth of the Muddy Fork valley where it joins the main Sandy River valley (Sec 14 and 15 T2S R8E). Over 1 m of lacustrine deposits in the form of interbedded sand, silt and organic debris indicates that the lake existed for at least a few years. The fine-grained sediment supports a dense growth of deciduous trees, mostly alders, very different from the dominant fir cover of the surrounding region, making the extent of the lake readily apparent. This broad-leaf forest covers about 0.3 km^2. The valley floor of the Muddy Fork was carpeted by a mature cedar forest before the formation of the lake and over a hundred 30 to 50 m high snags drowned by the impounded water are found within the lake deposit boundaries.

The second lake, at the mouth of Lost Creek (Sec 21 T2S R8E), is not nearly as well defined as the Muddy Fork lakebed. Its existence is suggested by sand and silt deposits that appear to be of lacustrine rather than fluvial origin. Lost Creek is much steeper in gradient than the Muddy Fork so the lake would have covered less area. No snags were found in the area but logs were found buried in the lacustrine deposits.

No Old Maid-age lahar deposits were positively identified below Marmot Dam. However, thick sand beds found near Dodge Park, Oxbow Park and near Troutdale may be terraces formed by a lahar runout or post-lahar flow with high sediment concentration. The deposits at Troutdale are up to 6 m above modern water level, much higher than normal flood deposits, and are at least 3 m thick.

Along the Zigzag River deposits of an Old Maid age lahar mantle the terrace of the Zigzag-age lahar sequence to an average depth of about 1 m and a maximum depth of 1.8 m. This sandy-matrix cobble lahar contains clasts up to 30 cm with an average clast size of 5 to 10 cm. As in the Old Maids Flat area, the lahar buried and killed a mature cedar forest, leaving standing snags up to 5 m tall. These snags have been dated at 270 ± 150 years BP. This date is from the outermost layer of wood from one of these snags, but the bark and an unknown number of annual rings have been lost to decay. The actual age of the lahar is therefore younger by an undetermined amount.

Downstream from the terrace, where the Zigzag River valley broadens and flattens, there is an obvious vegetation zone very different from the surrounding forest. Unlike the surrounding flora of Douglas fir, ferns, rhododendrons and huckleberry, this zone is sparsely covered by stunted pines 10 to 15 cm in diameter with little or no undergrowth. This type of vegetation is very similar to that found growing on the Old Maid-age lahar surface on Old Maids Flat. It is the result of lack of soil formation owing to its youth and the relatively dry subsurface conditions caused by drainage through the sandy lahar deposit. This "dry" vegetation zone extends for about 1 km onto the flat area of the Zigzag River valley (Sec 17 T3S R8E) and probably represents the path of the distal portion of the Old Maid age lahar.

Physical Characteristics

Although only a single lahar is recorded in deposits along the Sandy and Zigzag Rivers, it was not necessarily the same lahar in both rivers. Radiometric dating of wood from the lahars gives about a 50-year range for emplacement (250 and 220 ± 150 years BP for the Sandy River deposits and 270 ± 150 years BP for the Zigzag River deposits) and the dendrochronologic and historical material extends that range to 90 to 100 years. It is possible that multiple Old Maid-age lahars were produced over a span of time and that only two, along separate rivers, produced overbank deposits which have survived to the present.

The smaller size and extent of the Old Maid age lahar (compared to the Timberline age lahars) produces a corresponding smaller clast size and range. Maximum clast size in the Old Maid age lahar is 0.5 m in the upper reaches of Old Maids Flat and 0.3 m near Brightwood, at the distal portion of the lahar. Average clast size for the two locations is 0.2 and 0.1 m, respectively.

Clast lithology was subdivided into 3 groups based on "hand lens" petrology: grey matrix dacite, black matrix dacite and "other rocks." Both types of dacite are aphanitic-porphyritic with phenocrysts of plagioclase and amphibole. Maximum phenocryst size is 3 to 5 mm for the plagioclase and bimodal 1 to 2 and 3 to 5 mm for the amphibole needles. The grey matrix dacite is generally more vesicular with up to 10 percent void space, some of the voids being plastic pull-aparts with numerous glass needles. Grey matrix dacite makes up 30 percent of the clasts by number. The black matrix dacite generally has 0 to 5 percent angular void space and makes up 65 percent of the clasts by number. Clasts with poorly developed breadcrust or radially fractured textures are common in both dacites. The remaining 5 percent of the clasts are classed as "other" rock types and include red matrix dacite and highly altered rock types incorporated into the lahar during flow, probably as it passed over the upper reaches of the main Timberline-age debris fan.

Depth of Old Maid age Lahar During Flow

All Old Maid age lahar deposits are veneers on pre-existing terraces and represent open-reach-type deposition. Actual peak-flow height was probably 1.5 to 2 times the deposit thickness. In virtually all locations this would give a flow depth of 0.8 to 1.5 m above the terrace surface. The bulk of the flow remained within the channel. The flat-topped nature of the terraces allowed the flow to travel up to 0.5 km beyond the channel in some places on Old Maids Flat.

Summary

During the last 10,000 years, at least 3 major eruptive periods have occurred at Mount Hood. The oldest, and volumetrically largest, the Timberline eruptive period, occurred between 1400 and 1800 years BP. The Zigzag eruptive period, volumetrically the smallest of the three, occurred between 400 and 600 years BP. The Old Maid eruptive period occurred between 180 and 270 years BP and its aftereffects may have been witnessed by early explorers.

The combined clastic debris from these periods buried the southwest flank of the mountain, producing a smooth debris fan. Lahars travelled at least 90 km and pyroclastic flows at least 13 km from their source area near Crater Rock. Flow-depths of the lahars probably averaged 8 to 12 m in most cases.

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Habitat Relationships of Wintering Passerines in the River of No Return Wilderness Area of Central Idaho

Abstract

Populations of wintering passerine birds and vegetation structural attributes were sampled in five vegetation types within the Big Creek Drainage, River of No Return Wilderness Area (now the Frank Church River of No Return Wilderness Area), central Idaho, in 1980 and 1981. Species occurrence differed between the two years. Most species used two or more vegetation types, with forested habitats receiving more use than open habitats. Stepwise discriminant analysis identified which of 21 vegetation variables were associated with presence or absence of bird species. No consistent patterns emerged to suggest that birds may have selected habitat in response to specific structural features of vegetation. We suggest that food supply may require birds to be opportunistic in their use of habitats in winter, and this opportunism may be reflected in the patterns observed in the Big Creek Drainage.

Introduction

Numerous studies in temperate North America have focused on the habitat use patterns of birds during the breeding season. Results have shown strong relationships between species abundance and structural characteristics of the habitats used. Studies of wintering passerines and their patterns of habitat use are comparatively few, especially in remote areas offering pristine habitat conditions.

A study of wintering passerines was conducted in 1980 and 1981 in the River of No Return Wilderness Area of central Idaho. We sampled bird species abundance and habitat characteristics in five vegetation types to determine what species wintered within the area; what patterns of habitat use were exhibited; and whether patterns of use could be related to structural characteristics of vegetation.

Methods

The study was located along Big Creek, a major tributary of the Middle Fork of the Salmon River. Field work was based at the Taylor Ranch, a wilderness facility operated by the University of Idaho. The terrain in this area is rugged, and winter weather can be severe. The topographically diverse terrain supports a mosaic of vegetation types, of which five were selected as representative of the study area. These vegetation types were: (1) open Douglas-fir (*Pseudotsuga menziesii*) forest; (2) closed Douglas-fir forest; (3) riparian woodland of black cottonwood (*Populus trichocarpa*), Douglas-fir, water birch (*Betula occidentalis*), thinleaf alder (*Alnus incana*), and Rocky Mountain maple (*Acer glabrum*); (4) shrubfields of sagebrush (*Artemisia tridentata*) with interspersed grasses; and (5) bunchgrass meadows of *Agropyron spicatum, festuca idahoensis,* and forbs.

A fixed-radius plot method (Dawson 1981) was used to obtain count data for birds. Transect lines totalling 2000 m were established within each of the five vegetation types. Permanent bird count stations were established every 100 m. In 1980, counts were initiated in late January and terminated in mid-April, with the arrival of spring migrants and summer residents. Sampling in 1981 extended from mid-January to early April. Counts were restricted to daylight hours (0630-1600). No counts were conducted during conditions of snow or rainfall, or if wind velocity exceeded 6 km per hour. All birds detected within 50 m radius of each station were recorded during a 3-minute period. Information recorded for each bird observation included station number, time of day, species, distance from observer, and type of detection (audial, visual, or both). Temperature, wind velocity, and percent cloud cover were recorded periodically. Each vegetation type was visited 10 times in 1980 and 7 times in 1981. Direction traveled along transects was reversed on successive visits.

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Each bird station served as plot center for a vegetation sampling plot of 50 m radius. Subplots were used to sample vegetation strata within the main plot (Figure 1). Species, numbers, and height classes were recorded for shrubs. Diameter at breast height (DBH) was used to classify trees as saplings (< 10.5 cm), poles (10.5-28.1 cm), and mature trees (> 28.1 cm). Tree crown volumes were estimated following the method of Mawson *et al.* (1976).

The bird and vegetation data were analyzed by step-wise discrimination procedures (Klecka 1975) to test whether specific vegetation variables were associated with presence or absence of bird species. Only the most abundant bird species each winter, and the vegetation types where they occurred frequently, were used in the analysis.

Our source of nomenclature for birds was the A.O.U. check-list and supplement (American Ornithologists' Union 1982).

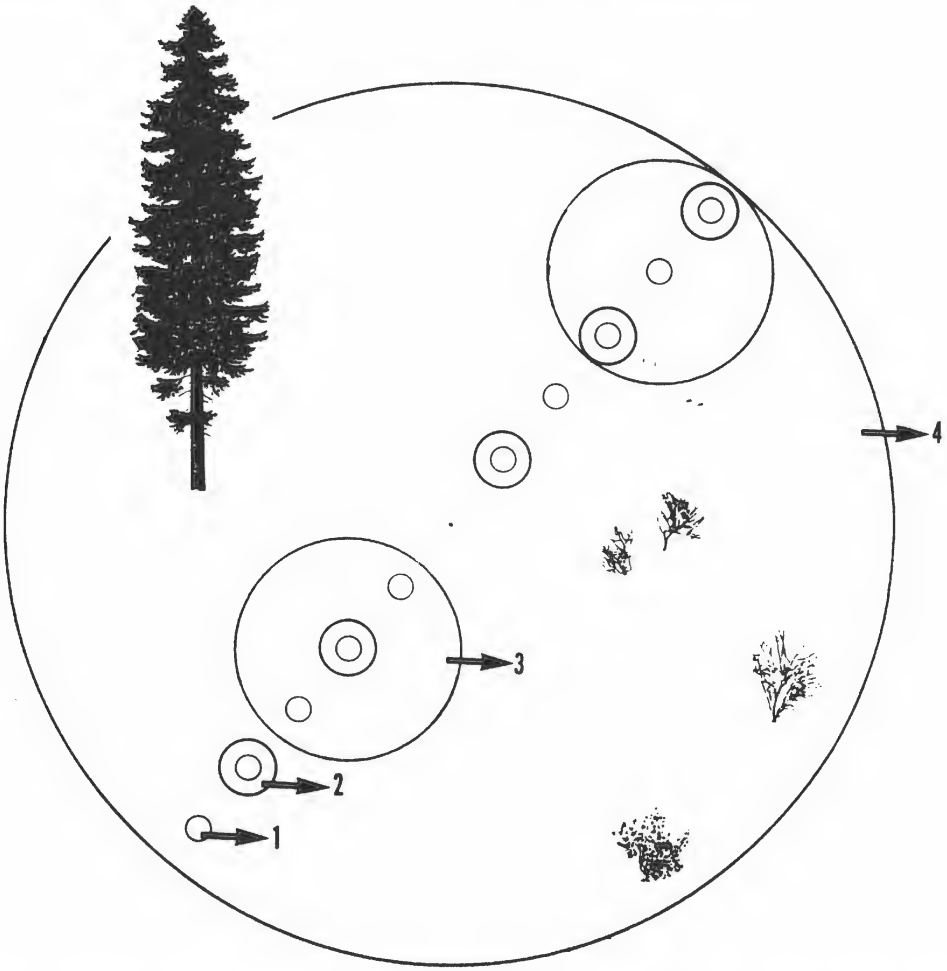

Figure 1. Schematic of nested plots used in vegetation sampling in each of 5 vegetation types. Numbers designate plots of differing radii and the life forms sampled: 1 = 4m², shrubs < 1.5m; 2 = 5.6m², shrubs > 1.5m; 3 = 12.6m², trees; 4 = 50m, the size of each bird census plot within which the vegetation plots were established.

Results

Obvious differences in bird species occurrence were observed between the two winters of the study (Table 1). In 1980, a total of 289 observations were recorded of 7 species. The 1981 counts yielded 508 total observations of 12 species. Less than half of all species were observed in both years. The two most abundant species in 1980, the mountain chickadee (*Parus gambeli*) and golden-crowned kinglet (*Regulus satrapa*), were observed much less frequently in 1981, and the Steller's jay (*Cyanocitta stelleri*) was not observed at all in the second year of the study. The two most abundant species in 1981, the pine siskin (*Carduelis pinus*) and red-breasted nuthatch (*Sitta canadensis*), had not been observed in the study area the preceding year. Other species appearing for the first time in 1981 were the black-capped chickadee (*Parus atricapillus*), song sparrow (*Melospiza melodia*), dark-eyed junco (*Junco hyemalis*), and red crossbill (*Loxia curvirostra*). The brown creeper (*Certhia americana*) was infrequently observed in all forested habitats in both years.

Wintering birds made greater use of forested habitats than of open habitats. Twelve species were observed in the riparian woodland, and 11 in each Douglas-fir forest type. Only the Clark's nutcracker (*Nucifraga columbiana*), black-billed magpie (*Pica pica*), and mountain chickadee were repeatedly observed in the open sagebrush-grass and bunchgrass habitats. Most species distributed their use over two or more habitats. The exceptions were the American dipper (*Cinclus mexicanus*) and song sparrow, which were observed only in association with riparian woodland.

Stepwise discriminant analysis was used to identify which of 21 vegetation variables that we had measured were associated with occurrence (presence or absence) of bird species observed. Significant relationships ($p < 0.05$) were found only for the open Douglas-fir and riparian vegetation types, and for an "overall" category that included all vegetation types in which a species occurred (Table 2). Eleven variables showed an association with presence or absence of the most abundant species in 1980 (mountain chickadee, golded-crowned kinglet) and in 1981 (red-breasted nuthatch, pine siskin). However, we did not find consistent patterns of association among the habitats in which a species occurred to suggest that birds may have selected habitat in response to the structural vegetation variables tested.

TABLE 1. Species and numbers of wintering birds observed in the riparian woodland (RW), open Douglas-fir (ODF), closed Douglas-fir (CDF), sagebrush-grass (SG), and bunchgrass meadow (BM) vegetation types of the Big Creek Drainage in 1980 and 1981.

	Vegetation Type									
	RW		ODF		CDF		SG		BM	
Species	1980	1981	1980	1981	1980	1981	1980	1981	1980	1981
Steller's Jay	8		7		2					
Clark's Nutcracker	3	4	2	7	3	17	8	2	2	
Black-billed Magpie			2		2		4	1	14	1
Mountain Chickadee	55	28	46	18	22	16	8	2		2
Black-capped Chickadee		2		1		3				
Red-breasted Nuthatch		16		24		52				
Brown Creeper	4	4	1	3	2	1				
Dipper	5	3								
Golden-crowned Kinglet	40	1	47	2	8		3		1	
Song sparrow		3								
Dark-eyed Junco		9		7		17		2		
Red Crossbill		1		9		9				
Pine Siskin		8		123		125				
Totals	115	79	105	194	39	240	23	7	17	3

TABLE 2. Habitat variables significantly related ($p < 0.05$) to presence (P) or absence (A) of the Mountain Chickadee, Golden-crowned Kinglet, Red-breasted Nuthatch, and Pine Siskin in the open Douglas-fir (ODF), riparian woodland (RW) and overall habitat categories of the Big Creek Drainage in 1980 and 1981.

	1980				1981			
	Chickadee		Kinglet		Nuthatch		Siskin	
Vegetation Variable	ODF	Overall	RW	Overall	ODF	Overall	ODF	Overall
No. trees	P							
Tree height								A
Tree DBH		P					A	
Tree crown density		P			P	P	P	P
Tree canopy volume			P		P	P	A	
No. poles		A	A			P	A	
Pole height					P		A	A
Pole crown density		P	P		P		A	A
Sapling crown density			P			A	P	P
No. shrubs <1.5 m			P	P	A			
No. shrubs 1.5-3.1 m	A		P			A		A

Discussion

In our study of wintering birds in the Big Creek drainage, we found patterns of species occurrence that were variable between years, indicated use of two or more habitats by most species, and suggested that habitat use was not strongly associated with specific structural features of vegetation. Other studies of wintering birds have suggested that food supply, and its interactions with environmental conditions, may be the most important factor affecting activities, local distribution patterns, and habitat use by birds in winter (Hilden 1965, Kricher 1975, Lack 1954, Smith 1980). If food is limiting, birds may be better able to survive by being opportunistic in their search for food within their winter range. This opportunism may be reflected in the patterns of species occurrence that we observed in the Big Creek drainage: bird occurrence may have been associated with patterns of food abundance, distribution, and availability that we did not measure.

We suggest cone production as one food-related factor that may have affected occurrence and abundance of certain species in 1981. Though not sampled, cones were conspicuously abundant in the study area in 1981 compared to the previous winter. The pine siskin, red-breasted nuthatch, red crossbill, and Clark's nuthatch are altitudinal migrants that have been reported to occur in association with locally abundant cone crops (Bent 1964a and 1964b, Burleigh 1972, MacArthur 1964, Smith 1980).

Differing weather conditions between the two winters of the study may have influenced food availability and, subsequently, occurrence of some species. In 1980, the study area was blanketed by a snow cover that persisted throughout the sampling period. In 1981, although average temperatures were lower, a snow cover was completely lacking throughout the study area. The difference in snow conditions between the two winters may explain why a ground-foraging species, such as the dark-eyed junco, was absent in 1980 but commonly observed in 1981.

In summary, our observations of wintering passerines in the Big Creek Drainage did not suggest that birds were using habitats in response to specific structural features of the vegetation. The need to locate food supplies may require birds to be opportunistic in where they occur, and in their habitat use patterns within these localities. Studies of food supply and food exploitation are needed to develop a better understanding of the habitat relationships of wintering birds.

Acknowledgments

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Counts, Coups, and Tally Marks: Evidence of Notational Systems in the Pictographic/Petroglyphic Record

Abstract

Count marks or tallies are common in the rock art of the Northern Plains. Analysis of eighteen sites on the middle Yellowstone River, including some petroglyphic records of considerable complexity, is consistent with a notational system of units and pairs. No internal evidence of ordering, sequencing, or further arithmetical evolution is yet discernible.

Introduction

Rock art on the Northern High Plains has been described as symbolic or representational, biographic, or ceremonial. That it may also be notational and ideographic has received little attention, largely because of the lack of a sufficient amount of comparative material. A survey of known and newly-discovered sites in south-central Montana in 1981-1984 alleviates this scarcity and leads on to problems in interpretation.

Rock art productions frequently include a series of "counts," "coups," or "tallies" associated with a representational or symbolic theme. These tallies may be obscure and easily overlooked, or they may be clearly delineated although enigmatically related to the other glyphs. When associated with battle scenes they might, for example, signify coup markers, kills, or enemies involved. When associated with hunting, animals, or symbolic glyphs, other numerical evaluations are possible. With little justification tallies have been called day counts, year counts, moon calendars, or astronomical notations. The marks may have represented some non-arithmetical idea, but the cultural provenance of many pictographs and petroglyphs is unknown, and there are no coeval texts. Thus, their meaning may never be established by external data. We are limited to such internal information we can discern in the glyphs themselves. This discussion is based upon the presumption that count marks may be arithmetic. A minimal interpretation rule suggests that perhaps a notational system of some kind is being represented, and on examination of a number of examples may allow some hypotheses about aboriginal numerical ideas—for instance, are counts unitary, decimal, or based on sets of 20 (vegesimal), or can other combinatory methods be descried? As an initial effort, 87 pictograph/petroglyph sites were recorded in detail. Of these 18 had count marks of some kind.

The Tally Mark and the Origins of Arithmetic

The keeping of counts has been a human concern across millennia. Perhaps what began an aide-memoir and an answer to the question "how many," became an end and a pleasure in itself, a mental product with a magic and reality all its own. Cultures became reflected in what was counted and what was not. Marshak (1972) described engraved count marks on bone and antler from the European Paleolithic and found them congruent with lunar observation. The Maya, preoccupied with time and its divisions, elaborated with dot ("one") and far ("five") into a numerical system with concepts of completion and zero, the ability to calculate in time units of 64,000,000 precise lunar-solar-venusian calendrics, a numerical foundation for the component names of men and deities, and intricate books of divination based on dates (Thompson 1971). Modern European mathematics seems to have begun with the counting stick ("tally") and simple "sets" (scores, hundreds, etc.), as Shakespeare remembers in Henry VI(2) Act 4 Scene 7, "our ancestors had no other books but the score and tally." The Peruvian *quipu* and *chimpu*, using knots or beads, achieved a similar accounting system based on units, tens, hundreds, and thousands which served the needs of an empire (Menninger 1969). The addition of a wire on which beads could slide and a mechanism for keeping track of sets as well as units produced the versatile abacus. Much encouragement that count or tally marks in pictographs might reflect

an arithmetic notational system comes from the meticulous analysis by Glossen and Marshak (1974) of a Chamula calender board on which the day counters, vertical lines of equal length and spacing, are arranged in horizontal series, much like those at 24ST560 in our sample.

In order that the descriptive material from the Yellowstone sites may receive principal attention in this discussion, a review of the continental or world-wide pictographic record is deferred. The variety of presentation and interpretation presents a major task in synthesis and suggests that an intensive rather than comprehensive approach may be more illuminating. Also deferred is the complex issue of the cultural affiliation of the artists who produced the drawings we will examine. More than a score of tribes are known to have hunted across the Northwestern Plains (Ewers 1968). A summary of pictograph/petroglyph chronologies is provided by Sundstrom (1984 p. 137-140). In the geographic bounds of our study, namely the middle reaches of the Yellowstone River, several investigators have addressed counts and counting. Mulloy (1958 p. 139) illustrated without discussion several "coup series" of marks and glyphs. Secrist (1960 p. 8) described a series of figures which may ultimately be shown to have an arithmetical significance. Conner and Conner (1971 p. 27-34) were among the first to discuss the occurrence of counts and figures-in-series. Keyser and Knight (1976 p. 608) noted that tally marks were the most common pictographic motif in western Montana and described dot series and their possible meaning. Keyser and Sundstrom (1984) give many excellent reproductions of count series in the Black Hills and a brief discussion of tally marks (p. 19). Beyond the presumption that count marks were somehow numerical these authors avoided an analysis of meaning.

What were the nomadic hunters of the Plains counting if that is what they were doing? How elaborate did their system become? Are their petroglyph marks recording anything more than "one count equals one thing"? Let us begin to look for answers in what seem to be the simpler examples. A battle scene at 24YL600 (Fig. 1) looks out over the Yellowstone River. Three men with shields are assailed by guns, spears, and arrows. On the left are 75 "tally marks" associated with two enigmatic marks. On the right is a series of 12 "counts." Adjacent panels, now dim, have many barely-discernible series of parallel arrows and guns, and a series of 35 vertical "tallies" each about 60 cm. long.

Another combat between a mounted man and one afoot at 24GV557 (Fig. 2) has 13 "tallies" arranged in a slanting pattern. A hand-to-hand encounter at 24YL418 (Fig. 3) has a superscript of three deeply-carved "tally marks." At 24YL70 (Fig. 4) three armed men stand before a double set of count marks, joined at the ends by vertical lines. At 24ST403 (Fig. 5) large count marks dominate small figures engaged in bear hunting and horse-riding. At 24YL434 (Fig. 6) a group of four armed men ride toward a tally series. At 24ML563 the cliffs bear a profusion of painted and incised glyphs in several styles. Interspersed are several sets of "tally marks," also in several styles (Fig. 7).

The bear panel at 24YL419 (Fig. 8) contains almost-terminally-eroded bears and shield-bearing men mixed with others that appear to be later, almost-fresh additions. There is an adjoining "superscript" panel filled with faintly visible count marks (not figured), the top series with ten vertical bars, each 20 cm., in a horizontal series. Below is a similar row of 22 marks, each 30 cm. tall, with a crudely outlined bear's head.

At Pillar Creek (Fig. 9) a man (inverted) with a lance stands beside two smaller figures and a continuing row of 21 objects which look like guns. Just above, four figures, two of which are incomplete and another which looks like a death bundle are in horizontal series with four "hairpin" (count marks connected at the top in pairs) and eleven count marks (pairs and units?). A red pictograph at 24CB630 (Fig. 10) shows more clearly an effort to use sets. Series of 16 dots, placed horizontally on an alcove wall is then repeated in 8 paired dots. Below 4 dots are placed in a vertical line, plus two half-moon shaped figures, perhaps? indicating a lunar count.

A "heraldry" panel of incised petroglyphs at 24YL419 (Fig. 11) is of count and symbol interest. At bottom left are two men in combat. Associated are two horizontal series and 37 lance-like objects and one gun. Some few of these are unadorned, but the rest have modifying details, none of which are identical. These include ornate "fans," projectile points, "feathers," varied-shape pendants, and perhaps individual

"medicine" or clan markers. The overall effect to the modern eye is of a hand-to-hand contest in the presence of a host of named individual observers, something like a heraldic tourney or the panoply of the Field of the Cloth of Gold. In any case, the glyphic panel does concern itself with an accounting, of some kind, of similar but recognizably individual objects.

A deep alcove 24ST560 in the upper reaches of Big Coulee Creek has a panel of black count marks (Fig. 12) which, are well-protected from the weather and exposed to sunlight only at the moment of sunset, and give an impression of antiquity. The panel is 276 cm. long, with 46 vertical bars, each 30 cm. Some have an enlarged head, others a bent foot. They were painted in black, evenly, without drip or run. The "brush" may have been a fingertip, or an implement of comparable size. The regularity of rendition suggests that they were done in one "sitting," (i.e. they do not seem to be accumulated over time). Small interstitial figures include five tailed circles, seven "horse hoof-marks" twenty-four "dots," four open squares or circles. Above are fourteen X marks, this series being interrupted by water damage and possibly being eighteen in number originally. The "coefficient glyphs" or "subsidiary notations" are enigmatic, as are permutations of 46 and 14 or 46 and 18. The cave overhang shades this glyph panel all day until just at sunset, and a rounded treeless hill due west cuts off the sunlight a few moments later (on 10 September 1983). No sighting mark was evident to suggest that solar equinoctial declinations were being observed, although the position was excellent for that purpose. The accompanying (also black) pictographs, some meters away, include a pair of humans in copulation, a man with spear and shield, a vertical series of eleven horizontal count marks, and a very nearly obliterated mounted spear-bearer.

Some ancient artists, instead of single-marks or tally strokes, used a series of depictions of the objects themselves. At 24ML562 (Fig. 13) men are "counted" by presenting rows of conventionalized man-figures. At 24YL82 (Fig. 14) a superscript above a spirited battle is a row of eleven tipis. At 24YL417 (Fig. 15) a group of seven guns hangs over another battle scene. Rows of horse hoofprints, perhaps counts, perhaps trails or direction indicators, occur at 24YL1189 (Fig. 16), 24YL402, 24YL600, 24YL1190 and 24YL419, where they wind through the "action" of the scene, and at 24YL704 where they are depicted in squared groups.

The pictograph at 24ST560, as noted, suggests a solar notation, while that at 24CB630 on similarly limited grounds, provokes question of a lunar record. Another, 24CB416 (Fig. 17 photograph) was pointed out by a landowner within the former reservation boundary. "The Crow used to call it a moon calendar," he said. The glyph seemed to be a number record laboriously pecked into extremely hard sandstone. It was composed of "units" of regular, carefully-formed, carefully-spaced, short, double, horizontal lines. These were in two vertical series, beginning 1.35 cm. above the cliff base. One series, extending 90 cm., had 23 of the double-horizontal units. The other series, inclined slightly from the vertical, has 17 "units." Below was a serpentine pecked figure which seemed to represent a horned dancer.

Discussion

"Tally" or "count" marks are common in the Plains petroglyphic record. Do they indeed represent an arithmetical notation and the mental processes which adumbrate it, or is the artist illustrating some other idea, quite unknown to us? If they are counts, what is being counted and why? In some glyphs the intended communication seems to be "how many" tipis or guns or men, but there is no evidence yet discerned of *ordering* or *sequencing* of units, the next expectable step in a number system. A third expectable step, a *grouping* of numbers, seems to be shown in two of our samples by way of pairs or "counting by two's." It is unfortunate for the hypothesis of a notational system that proof most likely will come, if at all, from internal evidence of the glyphs themselves. We can, so far, only presume for working purposes a rudimentary counting device of one mark for one object, with no further conceptual evolution, as in Mesoamerica, of notational sophistication; i.e., sets more complex than pairs, glyphic number conventions, calendric ideas, naming sequences, phonetic equivalents or time units. The very large number of sites yet to be analyzed, dated, and understood, and indeed yet to be discovered, may alter this appraisal.

Sites Described

24CB417	Kraus	24YL434	Horse-House
24CB630	Bear Two Shield	24YL82	Manual Lisa
24YL417	Doctordic	24YL419	Nordstrom-Bowen
24YL704	Chief Joseph	24YL1190	Pillar
24YL402	Alkali Creek South	24GV557	Northside
24YL1189	Canyon Creek	24ST403	Molt
24YL600	Custer	24ST560	Weppler #2
24YL418	Castle	24ML563	Signal Mountain
24YL70	Rossell	24ML562	30 Mile Station

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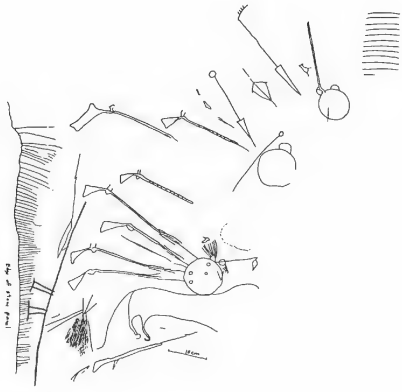

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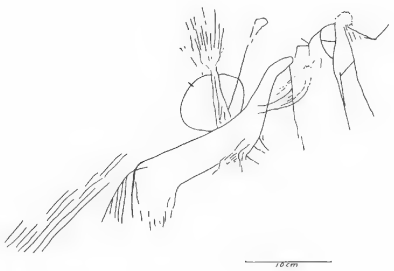

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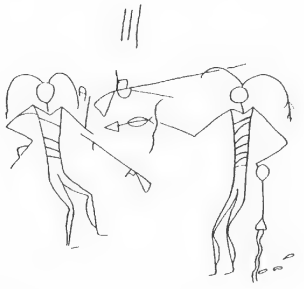

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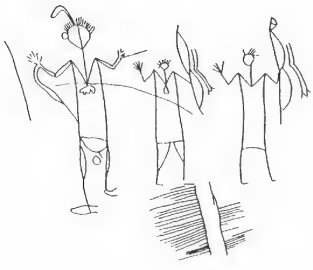

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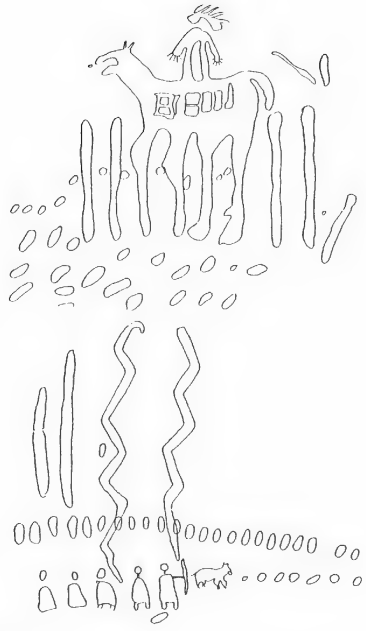

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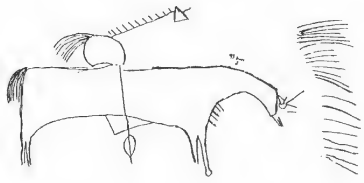

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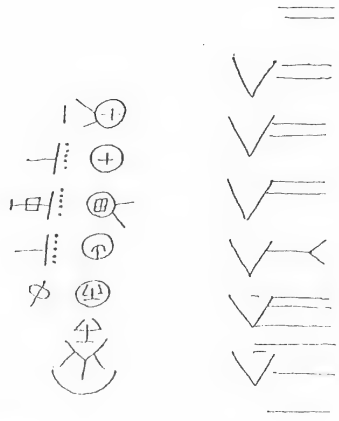

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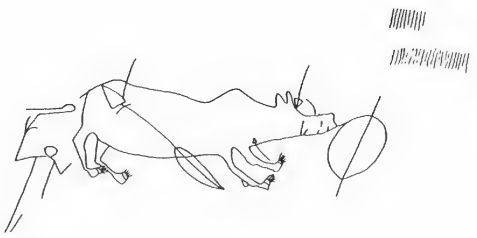

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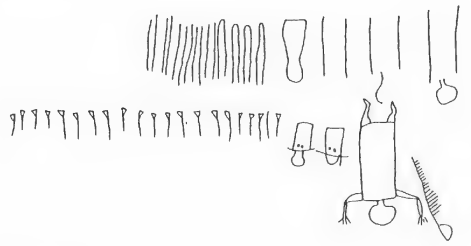

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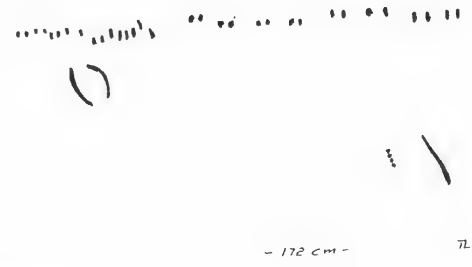

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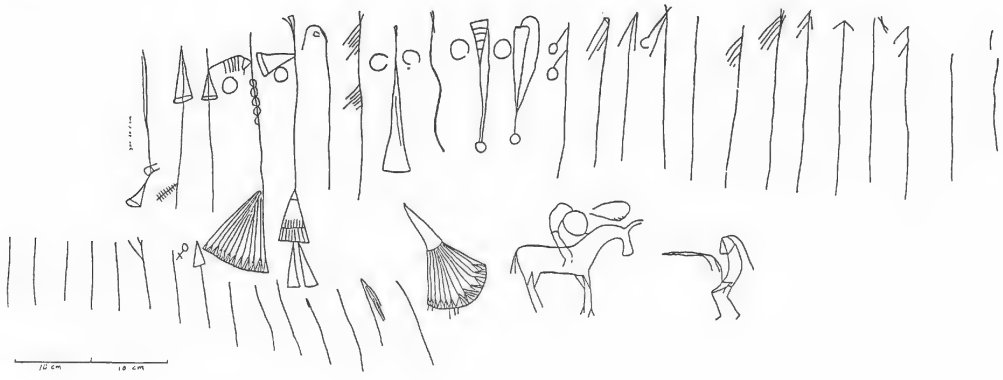

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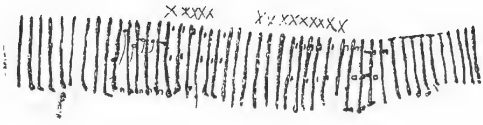

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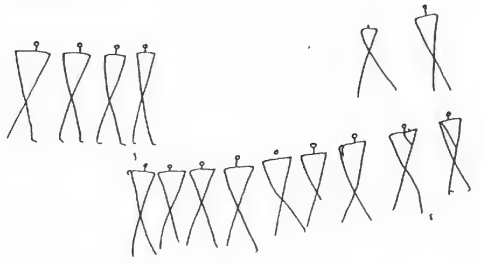


Figure 13.

Figure 14.

Figure 15.

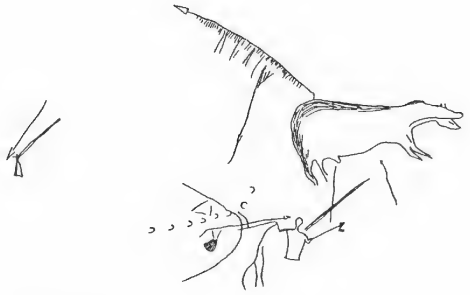
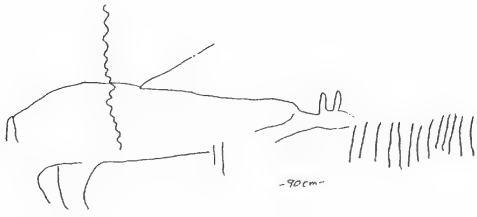


Figure 16.

Figure 17.



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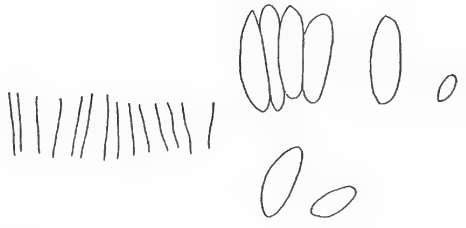

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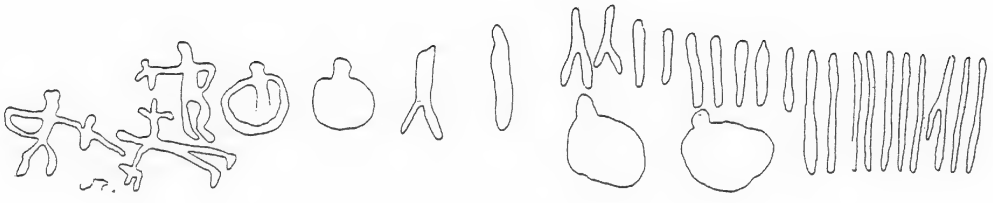

Figure 20.

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Seasonal Variation in Mycophagy by the Western Red-backed Vole, *Clethrionomys californicus,* in Southwestern Oregon

Abstract

We analyzed the fungal spore content of fecal pellets collected from western red-backed voles (*Clethrionomys californicus*) live-trapped between 1981 November and 1982 November in the foothills of the Cascade Range of southwestern Oregon. Nineteen fungal genera were identified, 17 of which were hypogeous mycobionts. *Rhizopogon* was the most frequently occurring genus. Statistically significant temporal variation occurred in spore abundance, number of genera per sample, and the relative abundance of each genus. Maximum fungus consumption occurred during late summer. Variation in mycophagy appears to be associated with seasonal changes in sporocarp abundance. Western red-backed voles apparently are hypogeous fungal generalists, foraging on sporocarps in direct relation to their availability.

Introduction

Until recently, little has been known about the food habits of the western red-backed vole (*Clethrionomys californicus*). Maser and Storm (1970) reported that *Clethrionomys* stomach contents consisted of finely chewed green material. Maser *et al.* (1978a) provided the first quantitative analysis of western red-backed vole stomach contents. They found that this species is highly mycophagous (fungus-eating), with 68 percent of the stomach contents by volume consisting of fungi. The majority of the identified fungi were hypogeous (below ground) fruiters; i.e. truffles and their relatives. Ure and Maser (1982) examined the stomach contents of two subspecies of *C. californicus* and three subspecies of *C. gapperi.* They found that *C. californicus* fed heavily on fungal sporocarps and lichens, and that the degree of mycophagy at higher elevations varied seasonally.

Small mammal mycophagy has important implications to forest management (Maser *et al.* 1978b). The majority of fungi eaten by the red-backed vole are ectomycorrhizal (Ure and Maser 1982). Mycorrhizal fungi form a symbiosis with vascular plant roots. Woody plants depend on mycorrhizae for adequate nutrient uptake. Mycorrhizae also increase longevity, size, and respiration rate of their host's roots and protect feeder roots against pathogens (Trappe and Fogel 1977). Hypogeous mycorrhizal fungi depend on mycophagy for spore dispersal (Trappe and Maser 1977, Maser *et al.* 1978b). Although the potential importance of spore dispersal by small mammals was noted over 30 years ago (Tevis 1952), its implications to forest management have not been widely recognized.

Although old-growth forests provide optimal habitat for the western red-backed vole (Tevis 1956, Gashwiler 1977, Franklin *et al.* 1981), red-backed voles occasionally occur in logged habitats if suitable microhabitats are maintained (Hayes 1983). The absence of *C. californicus* from clearcuts (Gashwiler 1959, 1970; Hayes 1983; Hooven and Black 1976) negates any significant role of this species as effective vectors of mycorrhizal fungal spores in clearcuts, but *C. californicus* may aid reforestation efforts through dispersal of spores in less disturbed logged habitats. Movements between suitable microhabitats could result in the dispersal of fungal spores into adjacent logged habitats.

We analyzed the spore content of feces from western red-backed voles captured over a 13-month period to examine seasonal variation in mycophagy. The analysis provides data on the

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amount and types of fungal spores transported via feces, the relative temporal variation in mycophagy, and phenology of hypogeous sporocarps.

Study Area

The study area is at ca. 900 m elevation in the foothills of the southern Cascade Range, Jackson County, 23 km northeast of Ashland, Oregon, T37S, R3E, Sections 19 and 20, Willamette Meridian. The slope ranges from 0° to over 35° with a predominantly east-facing aspect. Soda Creek, a small perennial stream, runs 40 to 100 m east of the study area.

The region is characterized by relatively mild, wet winters and hot, dry summers. Night temperatures are often low, and may drop below 0°C at upper elevations during summer.

The vegetation of the study area is old-growth forest in the mixed conifer zone (Franklin and Dyrness 1973). Douglas-fir (*Pseudotsuga menziesii*) is the most abundant tree species in the overstory and the most abundant conifer in the understory. Western redcedar (*Thuja plicata*), white fir (*Abies concolor*), and ponderosa pine (*Pinus ponderosa*) are the major overstory associates in approximate order of abundance. The understory is composed of a variety of broadleaf trees and shrubs including California black oak (*Quercus kelloggii*), Pacific madrone (*Arbutus menziesii*), poison oak (*Rhus diversiloba*), oceanspray (*Holodiscus discolor*), and red-flowering currant (*Ribes sanguineum*). Bigleaf maple (*Acer macrophyllum*) and Pacific yew (*Taxus brevifolia*) occur in moist areas.

Methods

We set 80 Sherman live traps (9 cm by 7.5 cm by 23.5 cm) in four parallel lines of 20 traps each, with intertrap intervals of 20 m. Interline distances were 20 m, 60 m, and 20 m. A small wad of cotton was placed in each trap, and the trap was covered with an aluminum shelter to mitigate the influences of temperature and moisture on the survival of captured animals. Each trap was baited with rolled oats. Traps were opened during nine trapping sessions between 1981 November and 1982 November for a total of 1840 trap nights (Table 1). No trapping was done in 1981 December, or in 1982 January, March, and October. Whenever possible, fecal pellets were collected from captured adult *Clethrionomys* with forceps as they were expelled form the anus and immediately placed in 2-percent formalin. A total of 163 samples was collected during the study.

Fecal samples were oven-dried for 24 h at 80°C and then weighed to the nearest 0.001 g. Each dried sample was macerated in 0.5 ml Tween solution (J. T. Baker Chemical Co., Phillipsberg, New Jersey). A drop of Melzer's reagent (Stevens 1974) was added to two to three drops of the Tween-pellet solution. One drop of this mixture was placed on the counting chamber of a hemocytometer and covered with a 22 mm^2, No. 1 glass cover slip.

Individual fungal spores present in each of the 320 squares comprising the central mm^2 of the hemocytometer grid were identified to genus. The total number of occupied squares per genus was recorded. The entire chamber was then scanned for less frequently occurring genera. Identification techniques are described by McIntire (1984).

Because differences in spore numbers could be a function of pellet size, the total number of squares per genus was divided by dry weight to obtain an index of spore abundance (SAI) for each genus in each fecal sample. Genera of fungal spores identified in the fecal sample, but absent in the counting area, were used in calculations of mycotrophic diversity, percent frequency of occurrence, and average number of genera per sample.

Relative abundance of each genus was calculated by dividing the sum of SAI values for a genus by the sum of SAI values for all genera in a given sampling period. Percent frequency of occurrence was calculated for each genus by dividing its frequency by the number of samples collected during that sampling period. Fungal diversity in the diet was calculated for each sample period using Shannon's (1948) diversity index:

$$H' = -\sum_{i=1}^{N} p_i \ln p_i$$

where p_i is the proportion of SAI values contributed by genus i and N is the number of genera identified in the sampling period. For diversity indices, genera present in the sample

TABLE 1. Percent frequency of occurrence of fungal genera in fecal pellets for each sample period.

Fungal genus	1981[1] NOV 22-24	FEB 19-20	APR 8, 22-23	1982[1] MAY 12-13, 20	JUNE 15-16, 22	JULY 28-30	AUG 22-23	SEP 25-26	NOV 22-23	Mean
Rhizopogon	87.5	33.3	28.6	45.0	100.0	93.9	66.7	81.2	85.7	69.0
Gautieria	18.8	26.7	21.4	40.0	11.1	46.7	47.6	56.2	35.7	33.8
Hysterangium	6.2	6.7	3.6	20.0	16.7	6.7	33.3	56.2	35.7	20.6
Leucogaster	18.8	6.7	7.1	15.0	--	26.7	42.9	31.2	7.1	17.3
Melanogaster	--	--	--	5.0	5.6	40.0	23.8	37.5	--	12.4
Calvatia	--	--	17.9	30.0	16.7	6.7	23.8	12.5	--	12.0
Hymenogaster	--	13.3	25.0	15.0	11.1	--	--	--	--	7.2
Hydnotrya	6.2	--	--	--	27.8	6.7	4.8	12.5	7.1	7.2
Martellia	--	--	--	--	--	20.0	19.0	18.8	--	6.4
Tuber	6.2	--	--	--	--	--	9.5	18.8	7.1	4.6
Octavianina	--	--	--	--	--	6.7	14.3	12.5	--	3.7
Microthecium	--	--	--	--	--	--	4.8	--	28.6	3.7
Geopora	18.8	--	--	--	--	--	--	--	14.3	3.7
Genea	--	--	--	5.0	--	--	--	--	14.3	2.1
Elaphomyces	--	--	3.6	--	--	6.7	--	6.2	--	1.8
Endogone	--	--	--	--	--	--	--	--	7.1	.8
Gastroboletus	--	--	--	--	--	--	--	--	7.1	.8
Genabea	--	--	--	--	5.6	--	--	--	--	.6
Glomus	--	--	--	5.0	--	--	--	--	--	.6
Number of genera	7	5	7	9	8	10	11	11	11	
Number of samples	16	15	28	20	18	15	21	16	14	

[1]No sampling was conducted during 1981 December, or 1982 January, March, October.

but absent in the counting area were arbitrarily assigned a value of 1 for each sample in which the genus occurred.

Temporal variation between sample periods in SAI values per sample was tested for statistical significance by the nonparametric Kruskal-Wallis test, and temporal variation in the number of fungal genera per sample was tested by analysis of variance. Arcsin transformation of the relative abundance data was performed to meet the assumption of a normal distribution (Snedecor and Cochran 1980), and analysis of variance with the transformed values was performed to test statistical significance of temporal variation.

Results

Spores of 19 fungal genera were identified in the *Clethrionomys* fecal pellets (Table 1). Spores identified as *Rhizopogon* and *Martellia* may include related genera that are morphologically indistinguishable. All but two of the identified genera are probably hypogeous mycobionts. *Calvatia* is always epigeous, and *Microthecium* is parasitic on *Geopora.*

Rhizopogon, the most frequently occurring genus, was present in at least 25 percent of the samples in all sample periods (Table 1). *Gautieria,* the second most frequently occurring genus, was found in over 25 percent of the fecal samples in two-thirds of the sampling periods. *Gautieria* and *Hysterangium* were present in the diet throughout the year. The only other genus with nearly year-round presence, *Leucogaster,* was absent in the June sample. *Hymenogaster* occurred from late fall through early summer but was most frequently found in the fecal samples collected in the spring. *Calvatia, Hydnotrya,* and *Melanogaster* exhibited bimodal frequency distributions, with one peak in early to late summer and one peak in the fall. *Tuber, Martellia,* and *Octavianina* were primarily present in the fecal samples during the late summer and fall. The remaining genera occurred in the fecal samples infrequently or sporadically.

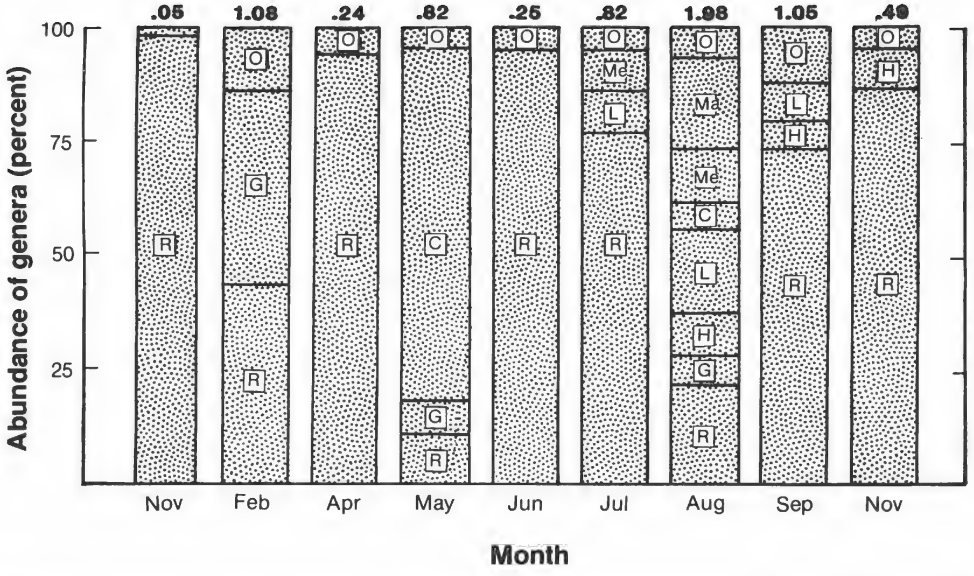

Figure 1. Relative abundance of genera and fungal diversity indices by sampling period. Genera contributing <5 percent are combined as "other." Fungal diversity indices are presented at the top of each bar. C = *Calvatia;* G = *Gautieria;* H = *Hysterangium;* L = *Leucogaster,* Ma = *Martellia,* Me = *Melanogaster,* O = other, and R = *Rhizopogon.*

The relative abundance of different fungal genera varied significantly by sample period ($F = 16.65$; $df = 16, 136$; $P<0.01$) (Fig. 1). *Rhizopogon* was the most abundant genus of mycorrhizal fungi in all sample periods and was the most abundant genus of all types of fungi in all sample periods, except May when *Calvatia* spores were more abundant.

Rhizopogon contributed at least 10 percent of the total spores in every sample period, whereas no other genus contributed >10 percent in more than one sample period. The disproportionately high SAI value for *Rhizopogon* in the November 1981 sample period in conjunction with low SAI values for other genera resulted in an extremely low diversity index (0.05). In August 1982, eight genera contributed at least 5 percent of the total number of spores, resulting in the highest diversity index value (1.98). No other sample period had more than three genera with each contributing more than 5 percent of the total number of spores.

The mean number of genera per sample exhibited statistically significant temporal variation ($F = 7.34$; $df = 8, 154$; $P<0.01$). The highest mean value (3.44) occurred in the September samples, and the lowest mean value (1.07) occurred in the February samples (Fig. 2).

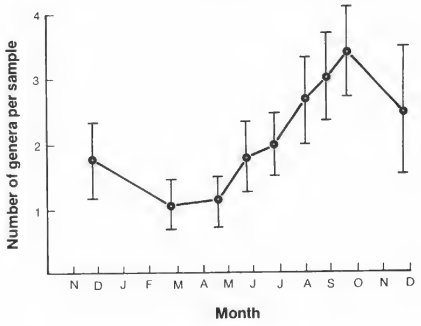

Figure 2. Mean number of genera per sample in fecal samples collected from red-backed voles trapped from 1981 November to 1982 November. Vertical bars represent 95 percent confidence intervals.

The SAI value of all genera combined per sample varied significantly by sample period ($H = 56.92$, $df = 8$, $P < 0.005$). The lowest mean value occurred in February, and highest value occurred in July (Fig. 3). The 1981 November and 1982 November samples had similar mean SAI values.

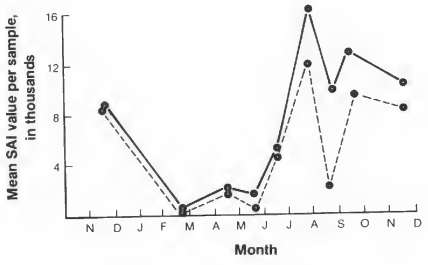

Figure 3. Mean SAI values per sample for all genera combined (solid line) and *Rhizopogon* (broken line) for fecal samples collected from red-backed voles trapped from 1981 November through 1982 November. SAI = spore abundance index.

The patterns of mean SAI values for *Rhizopogon* and the mean SAI values for all genera combined were similar for all sample periods except August when *Rhizopogon* SAI values decreased dramatically (Fig. 3). High mean SAI values for *Gautieria, Leucogaster, Martellia, Hysterangium,* and *Melanogaster* in the August sample accounted for this difference (Fig. 4). The mean SAI value of *Melanogaster* was relatively low in the September sample despite a high frequency of occurrence. *Calvatia,* the only genus of epigeous fungi present in the samples, exhibited a different pattern of mean SAI values than any of the hypogeous fungal genera. The mean SAI value for *Calvatia* was highest in May, when mean SAI values for hypogeous fungal genera were low. Except for mean SAI values for *Octavianina,* which were 390 for both August and September samples, mean SAI values for all other genera were less than 150 for all sample periods.

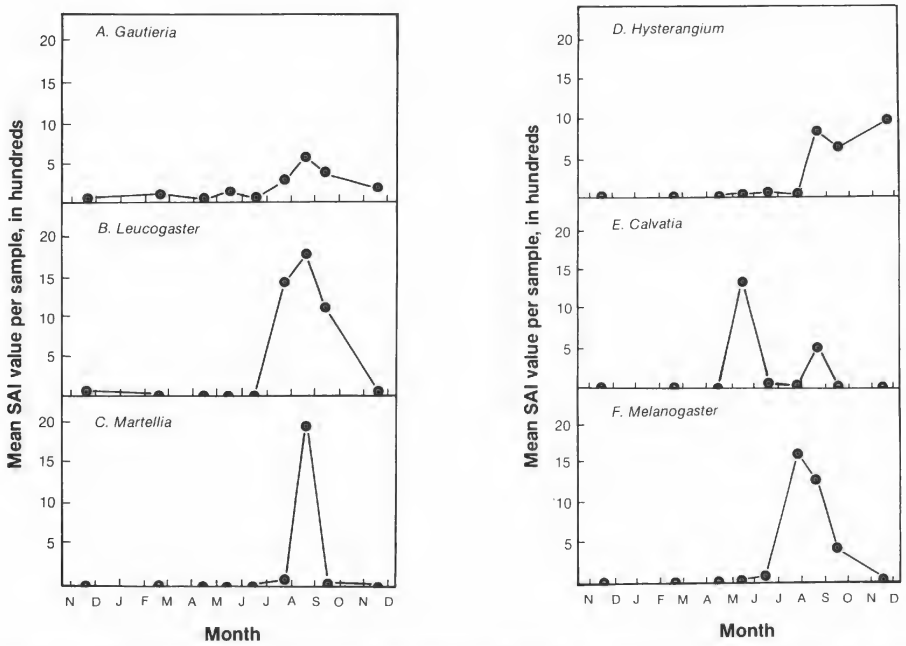

Figure 4. Mean SAI value per sample of six genera in fecal samples collected from red-backed voles trapped from 1981 November through 1982 November.

Discussion

Fogel (1976), working in the Oregon Coast Range, presents the only published data on hypogeous sporocarp abundance and phenology. Although species exhibited variation in fruiting phenology, the total mycorrhizal sporocarp population exhibited a bimodal productivity curve, with a spring peak in April to May and a fall peak in October to December. Spring sporocarp abundance increased logarithmically as the mean minimum air temperature increased from 0°C to 6°C. The decrease in number of sporocarps in the summer was attributed to a decrease in soil and litter moisture. Production of sporocarps in the fall increased with the onset of autumn rains until mean minimum air temperatures decreased to 4°C. Although Fogel noted that mycophagy may have influenced his estimate of production of sporocarps, he did not examine the relationship between mycophagy and sporocarp abundance.

The climate of our study area differs from that of Fogel's Coast Range site. Although no meteorological data were collected at our study site, data from Hyatt Reservoir, the closest active weather station (located 20 km south of the study area, T39S, R3E, Section 16, elevation 1500 m), can be used as an indication of meteorological trends for the general area. From 1981 November through 1982 May and in 1982 November the mean minimum air temperatures were below 0°C at Hyatt Reservoir (unpublished data, U.S. Weather Bureau, Medford, Oregon). These temperatures contrast with those during Fogel's three-year study, where subzero mean monthly minimum temperatures occurred only three times: 1972 December, 1973 January, and 1974 January. With the onset of autumn and winter precipitation at Hyatt Reservoir, mean minimum temperatures dropped below 0°C. Assuming similar meteorological trends at our study site, and that microclimatic effects on production of sporocarps are stimuli similar to those in the Coast Range, the primary fruiting seasons at our study site are relatively short. Low temperatures between the late fall and spring probably restrict sporocarp production, resulting in a unimodal sporocarp productivity curve with primary production in summer and fall.

The close association between observed SAI values and meteorological trends at Hyatt Reservoir corresponds with Fogel's observations concerning the influence of weather on sporocarp production. Spore abundance was lowest in the February through May samples, when monthly mean minimum air temperatures were below 0°C at Hyatt Reservoir. With a rise in the mean minimum air temperature above 0°C, the total number of spores increased dramatically in the June and July samples and remained relatively high through the November sample. This association suggests that in southwestern Oregon, *Clethrionomys* may consume hypogeous sporocarps in relation to their availability.

High SAI values occurred in both 1981 November and 1982 November samples despite mean minimum air temperatures below 0°C at Hyatt Reservoir during those periods. The higher-than-expected SAI values may have resulted from a delay between the cessation of sporocarp production and the time most of the sporocarps were consumed, as suggested by Ure and Maser (1982). An alternative explanation is that mean minimum air temperatures dropped below 0°C at our study site at a later date, extending optimal sporocarp production through November.

Although *Clethrionomys californicus* are fungus and lichen specialists (Ure and Maser 1982), we hypothesize that they are generalists in selection of available sporocarps. *Rhizopogon,* the predominant genus of fungi in the fecal samples, is also by far the most abundant genus of hypogeous fungus in coniferous forests of southwestern Oregon, fruiting most abundantly in the late summer and autumn months (J. M. Trappe, personal communication). In late summer and autumn, the diversity and abundance of other genera of hypogeous fungi increase dramatically. This pattern of sporocarp abundance is the same trend we observed for SAI values of different fungal genera.

These trends are similar to those exhibited by western red-backed voles in other areas in the Oregon Cascade Range (Ure and Maser 1982). In the Coast Range, however Ure and Maser (1982) found a different pattern of fungus consumption, with no apparent correlation between hypogeous sporocarp availability and the degree of mycophagy by western red-backed voles. They attributed the different pattern to an abundance of sporocarps that exceeded forage demand

during certain times of the year, and voles feeding on cached sporocarps when availability was low. In the Cascade Range, the shorter season for sporocarp production and corresponding paucity of sporocarps during certain seasons probably account for the closer relationship between sporocarp abundance and mycophagy by western red-backed voles.

In a study by Ure (personal communication), *Rhizopogon, Gautieria, Hysterangium,* and *Leucogaster* were the most frequently occurring genera, in descending order of frequency, in the stomachs of western red-backed voles from the Cascade Range. These genera also occurred most frequently in our study, in the same order of frequency. This contrasts to Ure's findings for the diet of Coast Range animals, which fed primarily on *Rhizopogon,* Hydnangiaceae, Endogonaceae, and *Gautieria. Rhizopogon* has also been identified as the major fungal constituent in the diet of other small mammals, including Siskiyou chipmunks (*Tamias siskiyou*) in southwestern Oregon (McIntire 1984), northern flying squirrels (*Glaucomys sabrinus*) in northern Oregon (Maser *et al.* 1985), and western gray squirrels (*Sciurus griseus*) in various locations in California (Stienecker and Browning 1970, Stienecker 1977).

McIntire (1984) hypothesized that hypogeous sporocarp distribution influences the distributions of some small mammal species. Similarly, western red-backed voles may select microhabitats that optimize opportunity for foraging on hypogeous sporocarps during months when sporocarps are abundant and select microhabitats that optimize utilization of other food resources, such as lichens, during other seasons. This phenomenon would be moderated or absent in areas in which sporocarps are more consistently available, such as the Coast Range.

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Peak Stream Discharge During Thirty Years of Sustained Yield Timber Management in Two Fifth Order Watersheds in Washington State

Abstract

Analysis of rainfall and peak flow from 1951 to 1980 by means of regression models was performed on two watersheds in southwestern Washington to examine the effects of timber harvesting on peak flow magnitude. One watershed contained timber between 45 and 60 years of age and had experienced no logging during the study period. The other watershed was being actively harvested and roaded at a rate of approximately 344 Ha/yr. From examination of regression models, no change in peak flow magnitude could be detected in either watershed for the 1951 to 1980 period.

Introduction

The results of watershed studies indicate that peak flows in rain-dominated systems of the Pacific Northwest have been shown to increase, decrease or remain unchanged after logging and road construction. Harr (1979) states that whether or not a change occurs depends on what part of the hydrologic system is altered and how permanent the alteration is. Clearcut timber harvest was implicated by Anderson and Hobba (1959) as increasing annual flood peaks through reduction in evapotranspiration and alteration in snow accumulation and melt rates. In initial hydrologic measurements in logged watersheds at the H. J. Andrews experimental forest (HJA), Rothacher (1970) found peak flows to have increased by some 200 percent due to increases in soil moisture after logging, allowing more water to be seen as runoff. In the Alsea Basin study, Harris (1977) reported a 20 percent increase in peak flow on Needle Branch Creek and a 2 percent increase on Deer Creek as compared to Flynn Creek, the control watershed, but considered such increases to be statistically insignificant since the mean of the peaks fell within the prediction limits. Hornbeck (1973), Har *et al.* (1975), and Ziemer (1981) also reported increases after logging due to differences in soil moisture. In further examination of HJA data, Harr (1979) reports that the normally large winter peak flow events, occurring after sufficient rainfall had occurred to restore soil moisture deficits, were similar between logged and unlogged areas. Peak flow increases were found to occur in fall and early winter storm events prior to soil saturation. Examining the effect of other forest practices, Harr *et al.* (1975) found increases in peak flow to be proportional to the percent of the watershed occupied by compacted soil areas (roads, landing, and skid trails) where increases were observed when compacted surfaces exceeded 12 percent of watershed area. Other observers have reported peak flows to be reduced by logging. Cheng *et al.* (1975) attributed peak flow reduction to be due to decreased soil pore space, thus forcing water through slower routes. Harr and McCorison (1979) demonstrated reduced peak flow in clearcut areas in western Oregon and attributed the reduction to be the result of decreased snow accumulation and increased melt rates. Christner and Harr (1982) examined long-term precipitation records for western Oregon and concluded that no significant climatic change had occurred over the last 35 years that could affect peak stream flow.

Such mixed results indicate that the particular hydrologic system in question must be well defined prior to interpretation of peak flow relationships. The majority of the peak flow research in the Northwest has been accomplished on watersheds ranging from 13 to 21 Ha in size. Because of the difficulty in quantification of hydrologic variables, peak flow relationships on larger streams have not been examined in as much detail as small watersheds. Lyons and Beschta (1983) detected an apparent trend toward peak flow increase in the Middle Fork Willamette river, a 665 km^2 watershed in Oregon, in association with a particularly heavy increase in logging activity. Increasing trends such as this are important in examining downstream response to logging activities, particularly in relation to

erosion of stream bed and banks, fish habitat, and flooding. This case study was undertaken in an attempt to evaluate whether the trends observed by Lyons and Beschta occurred elsewhere.

The objective of this study was to examine peak discharge in relation to timber harvest through use of historical stream flow records on two watersheds: one in a state of forest regrowth and the other having experienced a relatively rapid rate of harvest during the last ten years.

Watershed Characteristics

The Deschutes watershed is located in the foothills of the Cascade Mountains in southwestern Washington state. The Deschutes River flows in a northwesterly direction to Budd Inlet at the southernmost end of Puget Sound. Total watershed area encompasses some 429 km² of which 232 km² occur in the headwater area examined in this study. The principal salmonid species utilizing the river are Coho salmon (*Oncorhynchus kisutch*), Steelhead (*Salmo gairdneri*), and Cutthroat trout (*S. clarki*).

Elevations range from 100 m at the stream gauge to approximately 1120 m, of which 10 percent lies above 850 m. The winters are generally mild with the major precipitation occurring as rain from Pacific Ocean frontal systems. Snow accumulations of 25 to 40 cm occur for short periods above 850 m in elevation. Annual average precipitation ranges from approximately 130 cm in the lower basin near the stream gauge to 210 cm in the headwaters area.

The headwater portion of the Deschutes watershed consists of long straight "v"-shaped valleys and smooth steep slopes, commonly 70 percent (35°) and steeper. Soils are moderately deep (50 to 100 cm) to shallow (less than 40 cm) loams and clay loams developing from volcanic ash mixed with basalt, andesite, basaltic breccia, and welded tuff residuum with local inclusions of sedimentary rock. The lower watershed was partially influenced by continental glaciation during the last glacial period. Slopes are 30 percent (17°) or less and ridges are broad and smooth. Soils developed on the glacial silts, clays, and sand and gravel deposits are highly variable, ranging from clay with low permeability to highly permeable soils developing on glacial outwash. Soil stability is generally good, with one isolated area of earth-flow slump terrain associated with deeply weathered tuff and breccia rocks.

Douglas-fir (*Pseudotsuga menziesii*) is the principal timber species in the basin with western hemlock (*Tsuga heterophylla*) and Pacific silver fir (*Abies amabalis*) at the upper elevations. The area has been continuously harvested over the past 30 years (Figure 1) when some 11,344 Ha or 49 percent of the project area was harvested. Currently, stand age on 44 percent of the area is less than 15 years. Road construction has been continuous during the same period, resulting in a road density of 3.08 km/km². The major form of timber harvest has been clear cutting using high lead cable systems. During early stages of basin development, tractor skidding methods were employed on some of the more gentle terrain in the lower basin. Minimal site preparation activities have been required, with broadcast burning accomplished in areas of particularly heavy slash concentrations. All clearcut units have been regenerated with Douglas-fir.

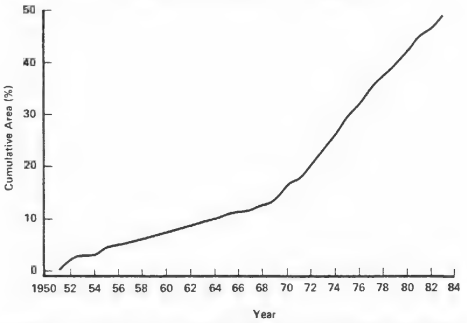

Figure 1. Cumulative area harvested in the Deschutes basin between 1951 and 1983.

The Naselle watershed occupies 141.9 km² on the southwest Washington coast in the southern portion of the Willapa Hills. The Naselle River flows in a southwesterly direction emptying into Willapa Harbor. Elevations range from sea level to approximately 760 m. Periods of snow are rare with the dominant precipitation occurring as long duration moderate intensity rain from north Pacific Ocean storm systems. A strong orographic enhancement is present with annual average precipitation ranging from 255 cm near the river mouth to 305 cm at the upper elevations.

The soils in the Naselle basin are deep and fine textured developing from weathered basalt,

fine-grained siltstone and graywacky sandstone rocks on steep slopes exhibiting a dendritic drainage pattern.

The principal timber species is western hemlock with some Douglas-fir and sitka spruce (*Picea sitchensis*). There was no timber harvest during the 30-year time period examined for this study. The stand age ranges from 45 to 60 years. Road density is 1.41 km/km^2 and no new road construction has taken place during the period over which stream flow data was examined for this project.

Methods

Peak flow data from the U.S. Geological Survey (USGS) gage near Rainier Washington was used for the Deschutes River. Continuous data was recorded at this site between 1949 and 1975 and a crest gage has been maintained since 1975. The Naselle River gage has been operative since 1929.

Peak flow was defined as the maximum instantaneous discharge above the established base flow for each stream. The base discharge levels selected by the USGS were 112 m^3/s for the Naselle and 56 m^3/s for the Deschutes. For this study, 67 peak flow events were identified on the Deschutes and 43 on the Naselle.

Storm rainfall corresponding to each peak flow event was obtained from representative National Oceanic and Atmospheric Administration (NOAA) weather stations. Storm rainfall was defined as the amount of rainfall on the day the peak flow occurred and the previous three days. Although there is no record of snow accumulation amounts, field observations since 1975 have shown that the larger stream flow events resulted from rain on snow.

Weyerhaeuser Company has been monitoring rainfall in the upper Deschutes watershed since 1975 with continuous recording instruments in conjunction with a streamflow monitoring network. To provide rainfall data for the years previous to 1975, correlations using monthly rainfall between nearby NOAA stations at Cougar, LaGrand and Olympia were made. The best relationship was obtained between the Weyerhaeuser gage and the NOAA station at Cougar 6E (r^2 = 0.94) 40 km south of the Deschutes basin (Figure 2). The relationship between individual storm events at Cougar and the Deschutes during the 1976 to 1980 period, when both stations were operative, produced an r^2 = 0.86 $p \leq 0.01$ (Figure 3). The largest precipitation event at both stations resulted from rain on snow.

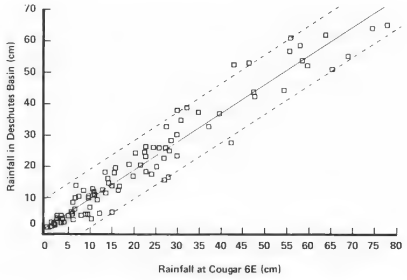

Figure 2. Relationship between total monthly rainfall in the upper Deschutes watershed and the NOAA station at Cougar 6E.
Rainfall Deschutes = 0.2685 + 0.9098 x rainfall at Cougar 6E r^2 = 0.94 ($p \leq 0.01$)

Rainfall recorded at the NOAA station located at the town of Naselle near the river mouth was used to characterize precipitation events for the Naselle watershed. No direct measurement of precipitation was available for the headwaters of the Naselle basin. Examination of an isohyetal map prepared from rainfall data from 1930 to 1957 by the NOAA river forecast center in Portland, Oregon showed the headwaters area to receive some 17 percent more average annual precipitation than at the river mouth (Anonymous, 1964). Since no other rainfall data were available, the rainfall recorded at the official Naselle station was used.

To examine temporal changes in peak flow magnitude in relation to land management, a regression method described by Lyons and Beschta (1983) which relates total storm rainfall to peak discharge was used to remove as much of the variation in discharge as possible attributable to rainfall, thus allowing temporal examination of the normalized data. Although there may be some shortcomings in this storm-rainfall-flow analyses since snow melt contribution could not be determined, unusually large precipitation or rain on snow events can be accounted for. A plot of the flow residuals against time was then used to examine the relationship between increasing clear-cut area and peak flow magnitude. Increasing values of the flow residuals in time would indicate increasing peak flows.

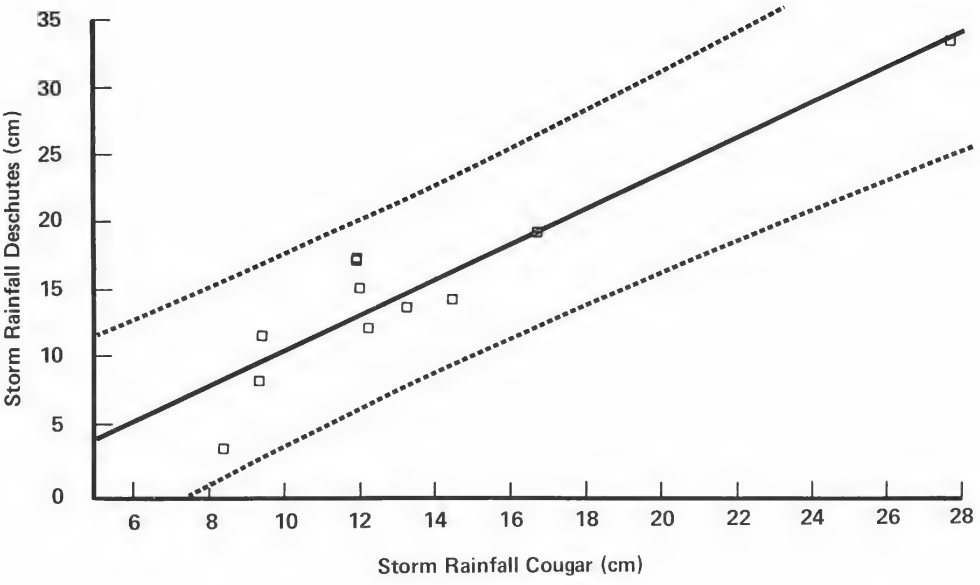

Figure 3. Relationship between storm rainfall at the Weyerhaeuser weather station in the Deschutes basin and the NOAA weather station at Cougar 6E. $r^2 = 0.86$ $p \leq 0.01$, 95 percent confidence limits indicated.

Results and Discussion

Regression of peak flow and storm rainfall events using a model of the form: $q = ax^b$ was performed for the Deschutes and Naselle river basins. While this model represented the data reasonably well, the r^2 was improved slightly by a linear relationship (Figures 4 and 5). This analysis showed that, although significant, less than half of the variation in peak flow magnitude could be accounted for by storm rainfall ($r^2 = 0.45$ $p \leq 0.01$ for the Deschutes and $r^2 = 0.34$ $p \leq 0.01$ for the Naselle) (Figure 4).

The large variance could be caused by inability to accurately account for the amount of storm precipitation contributing to the hydrograph peak and other factors, such as antecedent soil moisture, snow melt, and precipitation form and intensity. These parameters must be more rigorously quantified before developing general predictive capabilities. Lyons and Beschta (1983) reported a similar relationship ($r^2 = 0.38$), and found that the addition of a time variable into the equation was significant, suggesting a possible increase in peak discharge as timber harvesting progressed.

A plot of the flow residuals for both the Deschutes and Naselle watersheds showed no time trends in peak flow magnitude (Figures 6 and 7). From this analysis, differences in peak flow between an actively harvested watershed and one at or approaching hydrologic maturity could not be demonstrated.

This case analysis indicates that care must be exercised not to assume that changes in stream discharge necessarily correspond to a particular level of timber harvest. A wide range of hydrologic factors and the level and duration of their alteration must be considered. Secondly, watershed size must be considered in interpreting research results. It has been demonstrated in small watershed studies that peak flow has been affected by timber harvesting and the road network. Similar evidence does not exist for northwest river systems the size of the Deschutes and Naselle. Because of the normal progression in timber harvesting, only a small percentage of a large watershed is harvested at one time. Even with the increased rate of harvest in the Deschutes after 1970, it was distributed throughout the basin and unlike the harvesting effects demonstrated in small watershed studies, no

effect in peak flow magnitude could be detected. Care must be exercised in the use of models based on data from small watershed studies for the purpose of predicting conditions in large watershed systems since the results can be misleading.

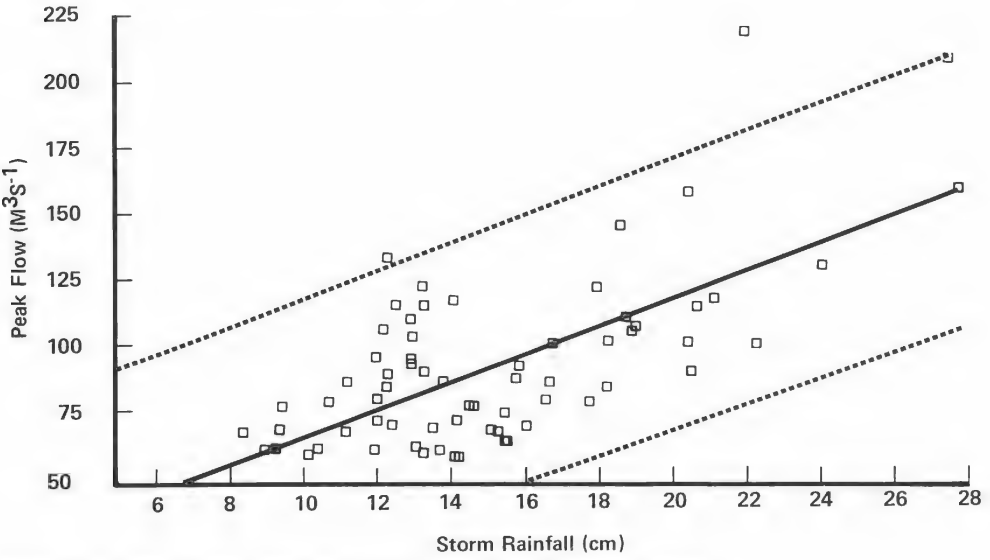

Figure 4. Relationship between peak flow and storm rainfall for the Deschutes watershed. $r^2 = 0.45$ $p \leq 0.01$, 85 percent confidence limits indicated.

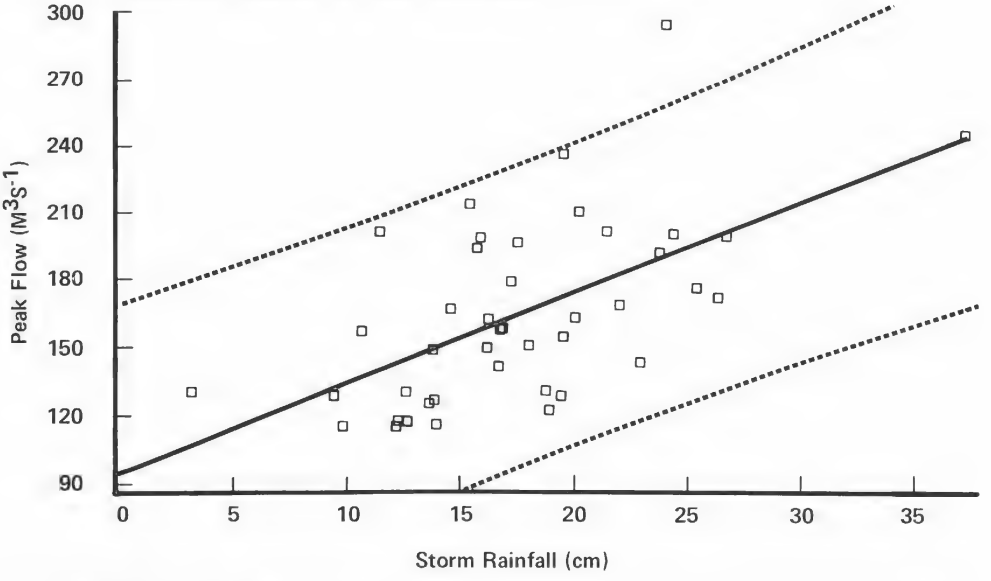

Figure 5. Relationship between peak flow and storm rainfall for the Naselle watershed. $r^2 = 0.34$ $p \leq 0.01$, 95 percent confidence limits indicated.

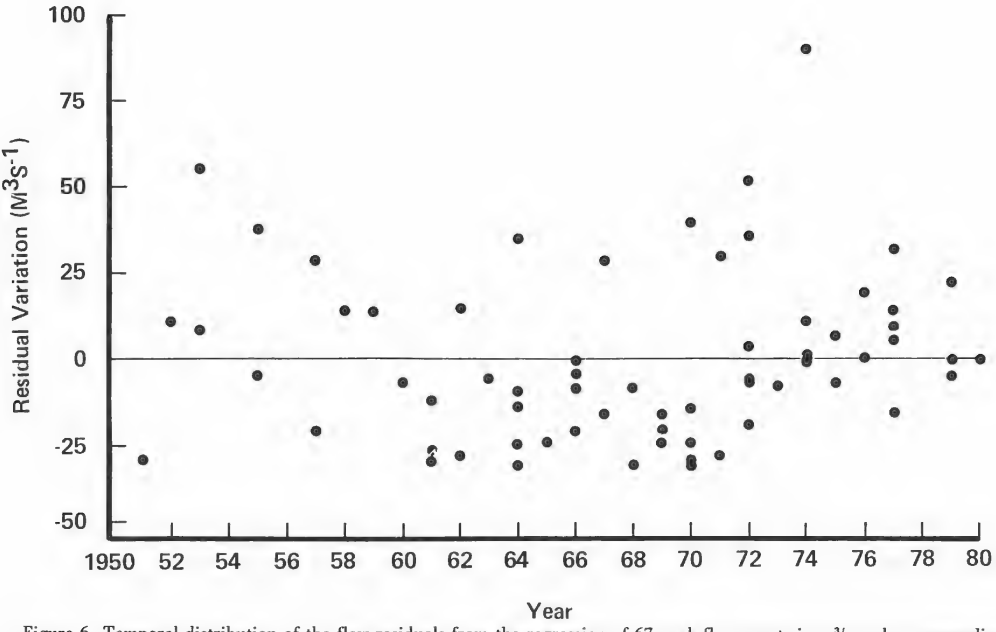

Figure 6. Temporal distribution of the flow residuals from the regression of 67 peak flow events in m^3/s and corresponding storm rainfall in centimeters for the Deschutes River basin.

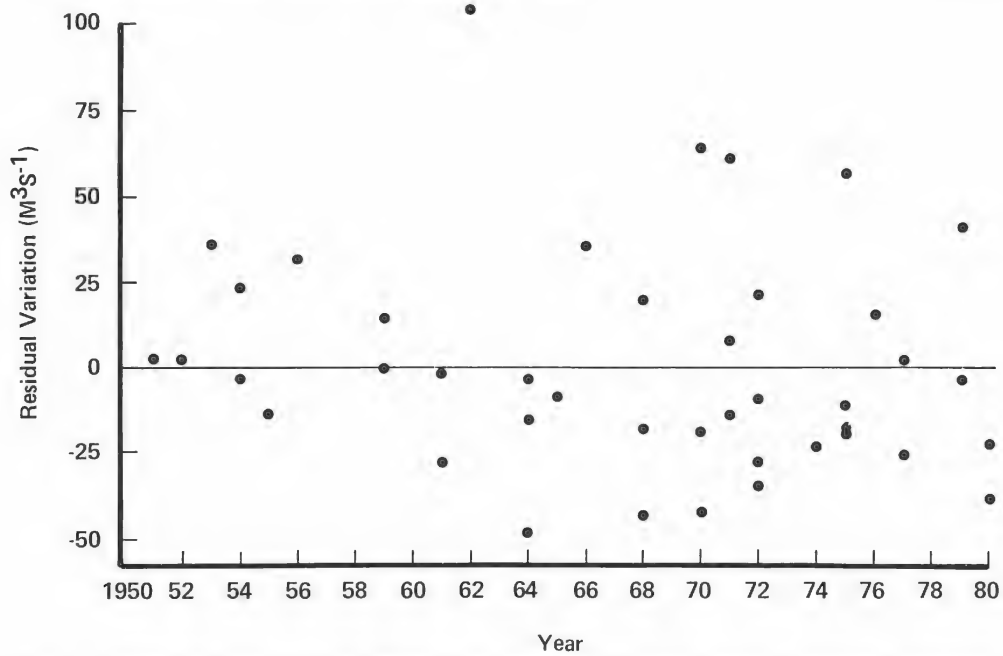

Figure 7. Temporal distribution of the flow residuals from the regression of 43 peak flow events in m^3/s and corresponding storm rainfall in centimeters for the Naselle River basin.

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Summer Diets of Domestic Sheep Grazing Mountain Meadows in Northeastern Oregon[1]

Abstract

Mountain meadows in northeastern Oregon are limited in extent, but are highly productive and can contribute substantial proportions of summer range forage for sheep. Proper range management depends in part on food habits information of animals using specific plant communities. Diets of domestic sheep grazing a dry mountain meadow during July and August were determined by microscopic examination of esophageal extrusa. Concurrent estimates of forage preference and availability were made. Sheep consumed nearly equal proportions of graminoids and forbs throughout the summer. Kentucky bluegrass was the most abundant graminoid in the diets and was preferred during both trials. Less available, but preferred grasses were timothy and prairie junegrass. Together, Northwest cinquefoil and velvet lupine comprised at least 50 percent of available forage throughout summer. Northwest cinquefoil was the most abundant forb in the diets but was not preferred. Velvet lupine was quite unpalatable and formed minor proportions of the diets. Field horsetail and yellow salsify were preferred forbs but contributed little to forage availability. Palatable species were more abundant in the diets on the first day of the trial than on the last because they were apparently consumed early, and became less available as the trial progressed. Daily changes for some forages in the diet were greater than changes between months.

Introduction

Proper rangeland management is partially dependent upon knowledge of livestock food habits. Such information allows manipulation of animals to meet their nutritional requirements and can be used to adjust timing of grazing to improve ecological integrity of the forage base. Food habits data of animals grazing specific plant communities are essential in developing models to predict carrying capacity, animal performance, and forage allocation among sympatric herbivores.

Although diets of domestic sheep (*Ovis aries*) have been studied on mountain meadows in Wyoming (May 1960) and southwestern Montana (Buchanan *et al.* 1972), no published data are available for the Blue Mountains Physiographic Province of northeastern Oregon. Here, rangelands provide three to four months of forage for nearly 100,000 sheep (Skovlin *et al.* 1976). Mountain meadows comprise only about 1 percent of total summer range in eastern Oregon and Washington (Rummell and Holscher 1955), but can produce 20 percent of summer range forage (Reid and Pickford 1946). Further, forage production on a hectare of mountain meadow is potentially worth 24-37 ha of average timbered range (Reid and Pickford 1946).

The purpose of this study was to determine: (1) diets and forage preferences of sheep grazing a dry meadow in the Blue Mountains Physiographic Province during early July and late August, and (2) daily changes in botanical composition of diets.

Study Area

The study was conducted on the Hall Ranch of the Eastern Oregon Agricultural Research Center near Union, Oregon (Figure 1). The study area was situated in the foothills of the Wallowa Mountains on a 15 percent north facing slope at an elevation of 1,128 m. Mean annual precipitation is 58.4 cm.

The 1.6 ha study area was fenced to create a 0.8 ha holding pasture and eight 0.1 ha experimental pastures. This pasture system was located on a "dry meadow" approximating the description of Hall (1973). Tufted hairgrass (*Deschampsia caespitosa*) typifies climax stands of such meadows (Reid and Pickford 1946). However, Hall (1973) could find none in this condition, presumably because most have deteriorated into other communities as a result of overgrazing

[1]This report is Oregon State Agricultural Experiment Station Technical Paper No. 7545.

(Franklin and Dyrness 1973). Reid and Pickford (1946) described four stages of deterioration: (1) perennial grasses, (2) perennial grasses mixed with perennial forbs, (3) perennial forbs, and (4) annual grasses. Vegetal cover was virtually uniform throughout the study area and was dominated by Northwest cinquefoil (*Potentilla gracilis*) and velvet lupine (*Lupinus leucophyllus*). Dominant grasses were Kentucky bluegrass (*Poa pratensis*) and timothy (*Phleum pratense*).

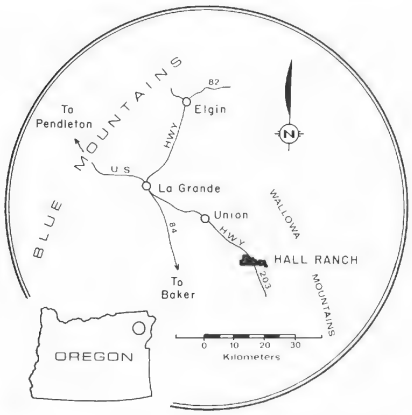

Figure 1. Location of the Hall Ranch near Union, Oregon.

Methods

Examination of esophageal extrusa is an accurate technique for determining diets of grazing animals (Rice 1970, Vavra *et al.* 1978, McInnis *et al.* 1983). Sheep used in this study were all mixed-breed yearlings. Esophageal fistulae were installed in six wethers and two ewes according to the procedures of Harris *et al.* (1967). Closure of these fistulae was accomplished using a removable stainless steel plate onto which was attached a separate rubber stopper. Dietary information was collected during two grazing trials: July 5-11 and August 19-25, respectively defined as early and late summer. Sheep were maintained on the holding pasture for five days before each trial. Following this adjustment period, two sheep were randomly assigned to each of four pastures where they remained for the duration of the trial. Four different pastures were used for the late summer trial. Water, salt, and shade were available at all times.

Prior to dawn of each of the seven consecutive mornings of both trials, sheep were outfitted with canvas collection bags and allowed to graze for approximately one-half hour. Esophageal extrusa was then collected, and preserved by freezing. Upon thawing, samples were squeezed in cheesecloth to remove saliva, and oven dried at 100°C for 72 hours.

Three microscope slides were prepared for each sample following the procedures of Sparks and Malechek (1968). Each slide was examined at the rate of 20 systematically selected fields at 100x magnification. Identification of plant species was based on comparison with epidermal characteristics of reference material. Frequency of occurrence of each species was converted to percent composition on a dry weight basis (Sparks and Malechek 1968). Dietary composition was averaged by pasture within days for each trial. Data shown are pasture means for all days in each trial. Factorial analysis of variance was used to compare differences among days and trials for each plant species at 95 percent and 99 percent probability levels, using a fixed effects model.

To estimate forage availability, 10 randomly selected 0.446 m^2 circular plots were caged in every pasture prior to both trials. Green weight of each protected species was estimated (Pechanec and Pickford 1937) immediately following the trial. Samples of each species were collected, weighed, oven dried at 100°C for 48 hours, and reweighed to establish dry weight conversions. Comparison of early vs. late summer forage availability was based on analysis of variance using randomized block design. Data presented are averages for all pastures.

A relative preference index of each forage species was calculated by obtaining the ratio of its mean composition in the diet to its mean composition on the meadow (Van Dyne and Heady 1965, Krueger 1972):

$$\frac{\bar{x}\ \%\ \text{dry weight composition in diets}}{\bar{x}\ \%\ \text{dry weight composition on meadow}}$$

These authors stated values greater than 1 indicate preference, while values less than 1 indicate avoidance. However, for these inferences to be statistically valid, it is necessary to estimate the error associated with each preference index value (Hobbs 1982). Thus, we constructed 90 percent confidence intervals about each preference

index, and interpreted the results as follows: plants for which endpoints of the interval exceeded unity were considered preferred; plants for which endpoints were less than unity were considered rejected; and plants for which endpoints were greater and less than unity were considered neutral (Hobbs 1982).

Results and Discussion

Eleven species of graminoids and 20 species of forbs were identified in diet samples. Table 1 lists species that comprised at least 1 percent of the diets during early or late summer. Sheep consumed roughly equal amounts of graminoids and forbs during both trials. There was no significant shift in consumption of these forage classes between trials despite significant declines in biomass from early to late summer (Table 2). Our results are consistent with Skiles (1984) who concluded sheep consume nearly equal proportions of graminoids and forbs. Preference indices for graminoids remained moderately high during both trials (1.8 and 1.9, respectively), and were significantly ($p < .10$) greater than unity (Table 1). Preference indices for forbs remained significantly ($p < .10$) less than unity during each trial.

Kentucky bluegrass, timothy, Northwest cinquefoil, field horsetail (*Equisetum arvense*), yellow salsify (*Tragopogon dubius*), and Oregon checkermallow (*Sidalcea oregana*), collectively formed at least 80 percent of the diets throughout summer. Kentucky bluegrass was the most abundant graminoid in the diets during both trials. This species was also the most productive graminoid on the meadow during the early summer trial. There was no significant change in the amount consumed from early to late summer despite a decline in availability. Preference indices for this species were significantly ($p < .10$) higher than unity during both trials and increased from 2.3 in July to 5.6 in August. The proportion of timothy in the diets increased significantly from 10 percent to 13 percent as summer progressed. The preference index for this grass declined from 2.3 during early summer to 1.7 during late summer, but was significantly ($p < .10$) greater than unity only in July. Prairie junegrass (*Koeleria cristata*) was preferred throughout summer, but was limited in availability and comprised only minor proportions of the diets. Sedges (*Carex* spp.) contributed substantially to the available forage base during July and August (28 percent and 42 percent, respectively, of total graminoid biomass). However, the preference index for sedges was a neutral 1.0 in early summer, and decreased to 0.3 by late summer.

Together, Northwest cinquefoil and velvet lupine accounted for at least 50 percent of total herbage biomass throughout the summer. Northwest cinquefoil was the most commonly consumed forb during both trials. However, preference indices for this species were 0.6 and 0.8 during July and August, respectively. Confidence intervals about these indices demonstrated lack of preference for this forb. Velvet lupine was absent from the diets during early summer, and comprised only 2 percent of late summer diets. Despite the abundance of this forb on the meadow, its slight occurrence in diets made it one of the least preferred forbs studied.

Some forbs were preferred even though their availability on the meadow was low. The preference index for field horsetail was 13.4 during early summer, and 6.9 during late summer. Yet, this forb made up less than 1.5 percent of available herbage on the meadow during either trial. Yellow salsify contributed less than 1 percent of total herbage availability during the July and August trials. However, this forb had the highest preference index of any species throughout the summer despite a significant decline in the amount consumed during late summer. Other preferred forbs were Oregon checkermallow and common dandelion (*Taraxacum officinale*).

Buchanan *et al.* (1972) found greater daily than seasonal changes in diets of sheep grazing mountain meadows in southwestern Montana for many forage species. Our results indicate a similar trend. While there was no significant difference between trials in total graminoid or forb consumption, daily amounts of these forage classes in diets shifted significantly as the trials progressed (Table 2). On the first day of the early trial, sheep consumed diets consisting of 34 percent graminoids and 66 percent forbs (Figure 2). By the last day, the proportion of graminoids increased to 64 percent and forbs declined to 36 percent. Sheep selected more palatable and easily available species early in the trial. As the trial progressed, these apparently became less available, and sheep consumed plants that had previously been less preferred.

TABLE 1. Dietary composition, herbage biomass, and preference of forage species comprising at least 1 percent of sheep diets during early and late summer.

	Dietary Composition[a] (percent Dry Weight)				Dry Weight Biomass[b] (kg/ha)				90 percent Confidence Interval and Preference Rating	
	Early		Late		Early		Late		Early	Late
	Mean	SE	Mean	SE	Mean	SE	Mean	SE		
Graminoids										
Kentucky bluegrass	25	1.9	26	2.2	145	11.0	46	3.4	1.2 - 3.4 (P)[c]	3.8 - 7.4 (P)
Timothy	10	1.0	13	1.2	59	18.0	74	40.5	1.0 - 3.6 (P)	0.1 - 3.3 (N)
Sedges	8	1.1	3	0.4	111	26.4	111	14.7	0.5 - 1.3 (N)	0.2 - 0.4 (R)
Prairie junegrass	3	0.6	4	0.4	13	2.7	9	1.2	1.5 - 4.5 (P)	3.5 - 5.3 (P)
Smooth brome	1	0.2	t[d]	0.06	2	1.3	t	t	−17.2 - 30.6 (N)	- -
Other grasses	5	0.4	3	0.3	60	25.7	25	1.6	0.0 - 2.2 (N)	0.7 - 1.7 (N)
Total Graminoids	52	3.1	50	2.9	390	55.0	265	36.5	1.4 - 2.1 (P)	1.5 - 2.5 (P)
Forbs										
Northwest cinquefoil	19	3.5	22	1.8	450	113.2	256	56.6	0.3 - 0.9 (R)	0.4 - 1.2 (N)
Field horsetail	9	1.8	9	1.4	9	5.7	13	7.5	3.2 - 30.0 (P)	2.6 - 11.1 (P)
Yellow salsify	10	1.4	5	0.8	5	1.8	3	0.2	12.2 - 41.2 (P)	9.9 - 23.0 (P)
Oregon checkermallow	7	0.9	9	1.3	44	9.8	27	6.7	1.3 - 2.8 (P)	2.0 - 4.5 (P)
Common dandelion	2	0.3	2	0.2	12	2.3	8	4.2	1.0 - 3.3 (P)	−2.4 - 7.4 (N)
Velvet lupine	0	-	2	0.4	218	35.5	299	70.0	- -	0.0 - 0.2 (R)
Other forbs	1	0.3	1	0.3	208	53.8	118	16.5	0.0 - 0.1 (R)	0.0 - 0.2 (R)
Total Forbs	48	3.1	50	3.1	946	63.8	724	91.4	0.6 - 0.7 (R)	0.6 - 0.8 (R)
Total	100		100		1,336		989			

[a]Based on 28 sheep diets per season.

[b]Based on 4 pastures per season, each subsampled with 10 plots.

[c]P = preferred; N = neutral; R = rejected.

TABLE 2. Results of analysis of variance for differences in dietary composition between trials and among days within trials; and herbage availability between trials.

Species	Dietary Composition			Biomass
	Trials	Days	Trials X Days	
Graminoids				
Kentucky bluegrass	ns[a]	*	*	**
Timothy	*	ns	*	ns
Sedges	**	ns	ns	ns
Prairie junegrass	ns	**	ns	*
Smooth brome	**	ns	ns	ns
Other grasses	*	*	ns	**
Total Graminoids	ns	*	ns	*
Forbs				
Northwest cinquefoil	ns	ns	ns	*
Field horsetail	ns	ns	ns	ns
Yellow salsify	**	**	ns	ns
Oregon checkermallow	ns	**	ns	ns
Common dandelion	ns	ns	ns	ns
Velvet lupine	**	*	ns	ns
Other forbs	ns	**	ns	**
Total Forbs	ns	**	ns	**

[a]ns, *, and ** respectively refer to not significant, significant at the 95 percent probability level, and significant at the 99 percent probability level.

Three species collectively formed 51 percent of the diets on the first day of the early trial: timothy (14 percent), field horsetail (15 percent), and yellow salsify (22 percent). These species were highly palatable, but totaled only 5.5 percent of the available forage. By the last day of the trial, this group of forages totaled only 19 percent of the diets. Dietary amounts of all three species declined significantly as the early trial progressed, but only yellow salsify declined significantly through both trials (Table 2). Preference indices for these species during early summer indicate high palatability throughout the trial. The daily decline in proportions consumed apparently reflects diminished availability as the trial progressed.

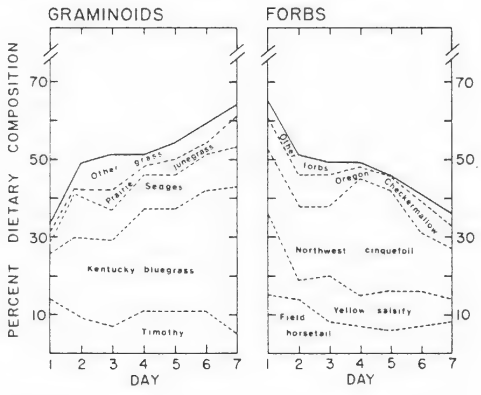

Figure 2. Daily changes in percent dietary composition of graminoids and forbs for the early summer trial.

Preference indices for Kentucky bluegrass, sedge, and Northwest cinquefoil on the first day of the early trial were 1.1, 0.4, and 0.5, respectively. Despite their low palatability, these species totaled more than 52 percent of available forage, and collectively formed 31 percent of the diets on the first day. As the trial progressed, proportions of favored species diminished in the diets and were replaced by less favored but more abundant species, notably Kentucky bluegrass. A similar, though less pronounced trend was observed during the late summer trial.

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Grasses in Young Conifer Plantations—Hindrance and Help

Abstract

Grasses often hinder the establishment of conifers in plantations by preempting resources, chemically excluding natural seedlings (allelopathy), attracting insects and animals, and increasing the fire potential. Grasses generally are not desirable in conifer plantations less than five years old, but after five years, they can aid conifer seedling growth by physically and chemically excluding more competitive vegetation. In plantations over five years old on good sites with deep soils, grasses can be beneficial by excluding deeper rooted shrubs. On poor sites with shallow soils, grasses and shrubs often compete throughout the profile and no benefit accrues to conifer seedlings by converting to grasses.

Introduction

Grasses in young conifer plantations often lead to conflicting points of view. Most foresters advocate little or no grass in conifer plantations. Most range managers favor at least some grasses, provided that they are palatable. Do grasses deter or enhance conifer seedling survival and growth? Should plantations contain grasses that lower seedling growth, but facilitate grazing? Or should plantations contain no grasses (or other competing vegetation) and therefore no grazing, but promote higher seedling growth? These questions reflect the need for information on conifer plantations when grasses are present or likely to be so. Needed even more is the understanding that grasses can both hinder and help. The key is to know when and where.

At an International Symposium on "Foothills for Food and Forests," held at Oregon State University in 1983, speakers from the United States, New Zealand, Australia, and the United Kingdom presented papers on how best to utilize the forage present in developing conifer plantations (Hannaway 1983). In the United States, studies on growing trees and livestock together are underway in several areas including the Pacific Northwest, California, and the Southeast. That opportunities exist for the production of forage while a conifer plantation is developing into a forest not only is a fact, but also is of great interest. Increasing production from the same land is attractive to a world ever in need of more food and fiber.

Ecologically, grasses are markedly successful worldwide. Over 5000 species have been catalogued—1500 species in the United States alone (Logan 1982). Not only are grasses extensive above ground, but they occupy much area below ground as well. Nearly 85 percent of the total standing crop of live plants in North American grasslands is below ground (Trappe 1981). The combined roots and root hairs of a single 4-month-old cereal rye plant grown in the laboratory had a total root surface area of 237 m^2 (2554 ft^2) and a total length of 623 km (387 mi) (Robbins and Weier 1950, 125-126). These values are many times greater than for conifer seedlings. Although rye grass plants develop much faster than most perennial grass seedlings, the magnitude of root and root hair development below ground demonstrates the strong competitive nature of grasses relative to young conifer seedlings. And some grasses begin root growth long before conifers, especially in cold soils. Capability to begin root growth early and to rapidly expand absorbing surfaces into large soil volumes allows the grasses to capture scarce moisture and nutrient resources. Fueled by these resources, shoot growth also is rapid. Together, grass roots and foliage preempt site resources to the point that conifer seedlings either cannot become established or, once established, cannot grow at the potential of the site.

Most plantations consist of planted or seeded conifers on ground denuded by some form of site preparation. In this disturbed environment, the opportunity for grasses to become established is great, especially if seed already is present or a seed source is nearby.

Grasses As A Hindrance

Grasses hinder seedling establishment in young conifer plantations by preemption of resources, allelopathy, attraction of insects and animals, and increased fire potential.

Preemption of Resources

In northeastern California, where soil moisture was the major limiting factor, Roy (1953) found that survival of planted pines varied with ground cover of shrubs and grasses. After two years, survival ranged from best to worst on bare ground with no stones, slash, open stony ground, shrub cover, and grass cover. Another study in northeastern California showed that 80 percent of ponderosa pine (*Pinus ponderosa* Dougl. ex Laws. var. *ponderosa*) seedlings died when planted in a sown mixture of one-year-old grasses (Baron 1962). Only 30 percent died when no grasses were present.

In a laboratory and field study on root competition between ponderosa pine seedlings and grasses in Arizona, grass roots grew faster than pine roots. Main roots of mountain muhly (*Muhlenbergia montana*) and Arizona fescue (*Festuca arizonica*) elongated 50 percent faster and consequently occupied a given soil volume sooner than pine roots. Root weights of grasses also were greater than pine seedling roots after two years (Larson and Schubert 1969). In a related experiment with the same grass species, most ponderosa pine seedlings, planted three months after the grasses, were suppressed or dead (Rietveld 1975). Furthermore, the two studies constituted "an awesome demonstration of the competitive power of fescue and muhly" (Rietveld 1975).

Scalping, or the removal of grasses and forbs from small areas around conifer seedlings, was evaluated on east-facing slopes in Mendocino County, California. Grasses and forbs were removed in 1.8-m and 0.9-m (6-ft and 3-ft) squares around Douglas-fir (*Pseudotsuga menziesii*) seedlings. The 0.9-m (3-ft) square was "not sufficient clearing of grasses and forbs to provide good survival" (Adams 1975, p. 15-17). A similar study of young ponderosa and Jeffrey pine (*Pinus jeffreyi*) seedlings in the foothills of the central Sierra Nevada showed similar results. Deep scalps 1.1-m by 1.2-m (3.5-ft by 4-ft) wide were created around seedlings in the spring. In June, survival was 93 percent and height growth excellent. By August, few seedlings were alive. Masses of grass roots from plants bordering the scalps had fully occupied the cleared areas, including the ground directly under the planted pines. Young grass plants also became established in the scalped areas and added to the competition. Together, the grass plants robbed the pines of essential soil moisture. Significantly, the tallest grass plants in the plantation were those bordering the scalps (J. L. Jenkinson, Pacific Southwest Forest and Range Experiment Station, pers. commun.).

Not only are conifer seedlings negatively affected by grasses, but so are conifer saplings and small poles. Growth of pole-sized pines on relatively shallow soils in eastern Oregon was hindered by bitterbrush (*Purshia tridentata*). After removing the bitterbrush, perennial Idaho fescue (*Festuca idahoensis*) invaded and decreased diameter growth of the pines even more (P. H. Cochran, Pacific Northwest Forest and Range Experiment Station, pers. commun.). In northeastern California, where relatively shallow soils predominate, different combinations of shrubs and grasses were created beneath a stand of pine poles. After five years, basal area growth of pines increased 28 percent over the control when grasses were removed and 6 percent when broadleaved shrubs were eliminated (Gordon 1962). Wright (1978) noted that similarly-sized stands in Arizona were partially thinned by grasses.

In these examples, reductions in conifer survival and growth can be attributed to preemption of scarce resources by the more aggressive grasses.

Allelopathy

Allelopathy is the process whereby a chemical substance released from one plant inhibits the presence or growth of another plant in the same or nearby habitat (Tukey 1969, Rietveld 1975). Allelopathic interaction between grasses and other plant species most often occurs when the other plants are small. Inhibition of germination and radicle or shoot elongation are typical.

Although extracts of many plants are toxic to other plants in the laboratory, few demonstrate toxicity in the field. Toxic metabolites in the

natural environment are neutralized by several factors, including adsorption on soil colloids, microbial activity, or possible inactivity because of xeric conditions (Tukey 1969). Grasses that show toxicity to conifer seedlings in the field are important to foresters and ecologists.

Few species of grasses, relative to the total number in the United States, have been screened for toxicity in the laboratory or field. Sixteen grasses (Table 1) have demonstrated toxicity in bioassays (Rietveld 1975, Heisey and Delwiche 1983). Most also are toxic in the field, or suspected of being so.

Allelopathy in grass and its effect on conifer seedlings is best shown in a study of ponderosa pine in Arizona (Rietveld 1975). A statistically significant reduction in pine seed germination rate, total seed germination, and initial radicle development took place from chemicals predominantly in live foliage, and to a lesser extent in dead residues of Arizona fescue and mountain muhly.

TABLE 1. Grass species known or suspected to be toxic in the field.

Common Name	Scientific Name
Foxtail fescue	*Festuca megalura*
Western wheatgrass	*Agropyron smithii*
Big squirreltail	*Sitanion jubatum*
Squirreltail	*Sitanion hystrix*
Cheatgrass	*Bromus tectorum*
Blue grama	*Bouteloua gracilis*
Timothy	*Phleum pratense*
Soft chess	*Bromus mollis*
Ripgut brome	*Bromus diandrus*
Medusahead	*Elymus caput-medusae*
Broomsedge	*Andropogon virginicus*
Threeawn	*Aristida oligantha*
Johnsongrass	*Sorghum halepense*
Bermudagrass	*Cynodon dactylon*
Sudangrass	*Sorghum sudanese*
Rabbitfootgrass	*Polypogon monspeliensis*

In the southeastern United States, loblolly pine (*Pinus taeda*) seedlings decreased in abundance and size if growing in fields of broomsedge (*Andropogon virginicus*). To ascertain the cause of this phenomenon, Priester and Pennington (1978) prepared live, dead, and decaying shoot extracts of broomsedge and applied them to four-week-old loblolly pine seedlings. The extracts of live and decaying broomsedge shoots significantly reduced pine stem, root, and needle lengths. Significant reductions in ovendry weight for both stem and root portions also were noted.

Toxicity can affect plant community composition. Community makeup often results from toxin production in some species and toxic tolerance in others (Muller and Muller 1956). In Oklahoma, for example, the annual grass threeawn (*Aristida oligantha*) effectively invades the early seral sunflower (*Helianthus annuus*) community because it tolerates the allelopathic environment created by the sunflower. In turn, threeawn dominates for several years by allelopathically suppressing nitrogen-fixing bacteria and blue-green algae, thereby rendering soil nitrogen levels too low to support species in subsequent seral stages (Wilson and Rice 1968). Such a process could affect plant succession and also conifer seedling growth.

Attraction of insects and animals

Site preparation and subsequent vegetation control measures often cause shifts in vegetation and population dynamics of associated organisms. On the west-facing slopes of Mount Shasta, California, thousands of acres of brushfield were cleared to establish conifer plantations. One large compartment was treated with herbicide to create fuel for broadcast burning. After a successful burn, ponderosa pine seedlings were planted. Several years later, shrub seedlings and sprouts were again treated with herbicide. Consequently, competing vegetation shifted from woody shrubs to grasses (*Bromus* spp. and *Stipa* spp.). Wingless grasshoppers (*Bradynotes obesa*) became epidemic. A year later, pocket gophers (*Thomomys* spp.) increased substantially. The shift from shrubs to grass and corresponding increase in grasshoppers and pocket gophers caused the loss of most of the pine seedlings (McDonald and Tappeiner 1985).

Competition from grass is commonplace in pine plantations throughout the southwest and is recognized as being important in reducing ponderosa pine survival and growth (Pearson 1942, Larson and Schubert 1969). Larvae of the southwestern pine tip moth (*Rhyacionia neomexicana*) also can reduce height growth of young ponderosa pines, sometimes by as much as 55 percent over a six-year period. And deformation

from repeated attacks can render seedlings worthless as crop trees (Jennings and Stevens 1982). Most attacks by this moth occur at heights less than 3 m (10 ft) above ground. Consequently, competition from grass and repeated insect attacks can keep pine seedlings below this height for years, each year compounding the loss of seedling growth.

On the Rogue River National Forest in southern Oregon, a native needlegrass (*Stipa californica*) became the principal herbaceous species in a ponderosa pine plantation. In spite of scalping around each seedling to control the grass and baiting to control the pocket gophers, survival after the first year was 25 percent. Grass invaded the scalped areas and the pocket gopher population recovered after the first growing season. After eleven years, less than one percent of the pines remained—over 1000 seedlings had been lost after the first year. Pocket gophers "were the main cause of mortality" (Hermann 1963).

The vole (*Microtus* spp.) also occupies grassy areas and poses a threat of damage to conifer seedlings. The Oregon vole (*Microtus oregoni*) is found in a wide range of habitats in the Pacific Northwest, especially on sites occupied by grasses and forbs common to logged or burned areas (Borrecco *et al.* 1979). Damage, in the form of clipped terminal and lateral shoots and basal debarking, can be serious in young conifer plantations (Lawrence *et al.* 1961, p. 16-17).

Increased Fire Potential

Converting ground cover in a plantation to one or more species of grass often increases fire potential. Moreover, the greater availability of resources resulting from the fire can allow the grass to gain in size and vigor.

On the east slopes of the Cascades, Blue Mountains, and northern Rockies, ponderosa pine is part of the climax community. Where grasses and some shrubs comprise the understory, fire frequency is estimated to be every 6 to 22 years. In the central Rockies, where the forest understory is predominantly grasses, fire occurs every 12 to 25 years. In contrast, fire frequency in the widespread ponderosa pine-bitterbrush community of west-central North America is estimated at 50 years (Wright 1978). These data indicate that predominantly grassy understories are associated with increased fire frequency, at least in ponderosa pine forests.

Relative to most shrub or tree communities, the spread rate of fire in grasses is often greater. A comparison of fire spread in tall grass and tall chaparral, for example, showed that fire moved 50 percent faster in grass (Albini 1976).

Fire frequency and spread rate are likely to increase when grasses are present in young conifer plantations. And fire may do more good than harm to the grasses. Increases in grass production, numbers, flowers, and seeds are likely within one year after burning, and recovery of perennial grasses is rapid.

Grasses As A Help

Grasses help conifer seedlings in young plantations by exclusion of competitive plant species and allelopathy.

Exclusion of Competitive Plant Species

As noted, grasses compete strongly with conifer seedlings, especially when the seedlings are small and not yet established. After establishment, which generally takes 5 years, grasses may actually aid conifer seedling growth. Although the grasses can negatively affect conifer growth, woody shrubs generally are even more competitive.

A well documented study in central California portrayed the potential that grasses have for controlling woody shrubs (Schultz *et al.* 1955). The shrub stand consisted of wedgeleaf ceanothus (*Ceanothus cuneatus*), chaparral whitethorn (*C. leucodermis*), deerbrush (*C. integerrimus*), and Mariposa manzanita (*Arctostaphylos mariposa*). It was burned in the fall. The following April, new seedlings numbered over 839,500 per hectare (339,500/acre). Ryegrass (*Lolium multiflorum*) and hardinggrass (*Phalaris tuberosa* var. *stenoptera*), each in a separate study, were seeded into the ashes just after the fall rains. A uniform stand of grass was established for each. In August, data showed that grass cover greater than 55 percent for ryegrass and 45 percent for hardinggrass eliminated all shrub seedlings.

Excavations in seeded and unseeded ryegrass plots related competition between grass and shrub seedlings to soil moisture. Where ryegrass had been seeded, shrub seedlings were 5

centimeters (2 inches) tall and roots had penetrated a maximum of 28 centimeters (11 inches). The ryegrass roots had grown downward 137 centimeters (54 inches). The soil moisture deficiency zone, as determined by the wilting point for sunflowers, extended down 122 centimeters (48 inches). In the unseeded plots, shrub seedlings averaged 20 centimeters (8 inches) in height and roots extended to a depth of 109 centimeters (43 inches). The soil moisture deficiency zone extended down only 15 centimeters (6 inches).

Near Mount Shasta, California, dense, mixed-species brushfields are being converted to conifer plantations. Here, a long-term ecological study has shown that a native needlegrass (*Stipa* spp.) invaded areas where the shrubs were removed. Once the grass became established, and this happened 5 to 6 years after the pines were planted, the plots that were initially free of shrubs still were free 18 years later. Shrubs from seeds produced on large plants in windrows nearby or possibly from dormant seeds in the soil, had not successfully invaded these areas (McDonald and Oliver 1984). The mechanism for shrub exclusion could be physical modification of the environment, emission of toxic substances from *Stipa,* or both. But whatever the process, the grass excluded the shrubs and resulted in statistically better height and diameter growth of the pines (30 to 375 percent better than control) (McDonald and Oliver 1984).

Two comparatively new studies in northern California also demonstrate the capability of grass to exclude shrubs. Both studies involved testing a number of manual and chemical treatments that were aimed at reducing shrub populations and enhancing conifer seedling growth. In one study, a species of perennial brome (*Bromus* spp.) had formed a dense stand where deerbrush had been eliminated. In the other, Pacific needlegrass (*Stipa californica*) and rescuegrass (*Bromus catharticus*) had become abundant where greenleaf manzanita (*Arctostaphylos patula*) and Sierra chinkapin (*Castanopsis sempervirens*) were killed. In both studies, the treated plots were about 0.04 hectares (0.1 acre) in size and surrounded by abundant seed producing shrubs. In addition, numerous dormant shrub seeds in the soil were an almost certainty. Yet, annual sampling has shown that once the grass became abundant, no shrub seedlings have become established. (Data on file at the Pacific Southwest Forest and Range Experiment Station, Redding, California).

The phenomenon of grass excluding shrubs was also noted in a fuelbreak study in central California. Part of the open fuelbreak prepared by a tractor was seeded with perennial grasses and part was left bare (Schimke *et al.* 1970). After five years natural regeneration, including ponderosa pine and whiteleaf manzanita (*Arctostaphylos viscida*), were abundant in the open area. Plants of these species were fewer and smaller when growing with grasses (Table 2).

In the cooler and more moist environment of the Oregon Coast Range, several clearcuttings were broadcast burned and seeded in the fall with perennial grasses and legumes. The grass mixtures were evaluated for effect on western thimbleberry (*Rubus parviflorus*) and red alder (*Alnus rubra*). Bentgrass (*Argrostis tenuis*) had the greatest impact on western thimbleberry, with all plots showing a significant reduction in both cover and frequency during the fifth year. Bentgrass and dwarf intermediate wheatgrass (*Agropyron intermedium*) had the greatest impact on red alder, with significant reduction of cover and frequency in the fifth year (Klingler 1982).

The impact of grass in reducing woody shrubs was also demonstrated in central and southern California. After wildfire, a standard practice is to sow annual ryegrass (*Lolium multiflorum*) as a ground cover for reducing runoff and erosion. In the relatively dry habitat of a large burn, *Lolium* cover reduced jimbush ceanothus (*Ceanothus sorediatus*) seedling density tenfold and slowed shrub height growth (Griffin 1982).

Allelopathy

Just as some species of tree seedlings are hindered by toxic substances from grasses, so do other species of seedlings benefit. Toxic substances from grasses can reduce competitive shrubs, undesirable trees, and even other grasses.

In one instance, toxic chemicals from bromegrass in old fields markedly reduced bromegrass seedlings (Meyers and Anderson 1942). But such documented examples are few, and more research is needed. As noted, only a fraction of grass species in the United States have been tested for emission of toxic chemicals, and an even smaller

TABLE 2. Characteristics of ponderosa pine and whiteleaf manzanita seedlings after 5 years in a grass and grass-free environment in central California.

Habitat	Density per .0004 hectare*		Height (centimeters)		Cover (percent)			
	Pine	Manzanita	Pine	Manzanita	Pine	Manzanita	Annuals	Perennial grasses
Natural	15.4	19.8	24.1	25.2	7.8	15.6	32.1	0.6
Grasses	1.9	2.2	13.2	13.5	0.2	0.3	19.2	64.0

*milacre

proportion of shrub and tree species have been screened for susceptibility to such chemicals. But the potential of grasses to help young conifer plantations also exists. Foresters and resource managers should be aware of this phenomenon and watch for examples of it.

Implications For Management

Survival and growth of young conifer seedlings depends on the availability of resources, especially soil moisture. In California and southwest Oregon, where long, hot, dry summers are typical, soil moisture usually is the limiting factor on nearly all sites, regardless of quality. Competing vegetation further reduces the already limited soil moisture resources. And the better site quality, the faster and more completely the site becomes occupied.

Given that grasses often are strong competitors, the question "How much grass is too much for conifer survival and growth?" often is asked. The answer depends largely on age of the plantation, soil depth, and degree of risk. Only general guidelines are presented, and exceptions are probable.

For newly planted conifer seedlings, one grass plant in a 1.8-m (6-ft) square (about 0.9-m or 3-ft radius) around the seedling early in the season is probably too much (McDonald 1983). The single plant likely will become a large plant with a root system larger than that of the conifer seedling. And after the production of seed, more grass plants soon will be present. Moreover, if one grass plant is present, the odds are that other seeds and plants of grass will be present and they too will mature and produce seed. For these reasons and because of extensive root development and capture of soil resources, grasses should be eliminated in young conifer plantations until the seedlings are established.

For five-year-old conifer plantations on medium-to-good sites, many grass plants per 1.8-m (6-ft) radius probably have less effect than many plants of woody shrubs. Medium and better sites usually are associated with soils over 0.9-m (3-ft) deep, and conifer saplings are less impacted by grasses than by deeper-rooted shrubs.

For five-year-old conifer plantations on poorer sites with soils generally less than 0.9-m deep, the relative rooting depth of shrubs and grasses is not as important. In general, roots of conifers, shrubs, and grasses grow through the soil to a rocky layer. Here, root extension becomes lateral and plants compete for resources on top of the rocky layer. No class of plants has an advantage.

Degree of risk is probably fairly high within a 0.9-m (3-ft) radius of bare ground around each seedling. Less risk is associated with a 1.5-m (5-ft) radius of cleared area. Early indications are that radii of 1.5 m (5 ft) or larger are required to control shrubs (Fiddler and McDonald 1984). The larger radii may be necessary to control grasses as well.

Increasing evidence suggests that early conifer seedling growth is closely related to amount of resources, especially to available soil moisture. Any moisture used by competing vegetation is that much less available for conifer seedling survival and growth. And given a limited amount of moisture, the advantage lies with those plants or species that are present first. Their roots are unimpeded by competitors' roots or chemicals or mycorrhizae, and they are free to exploit an increased soil volume. In turn, shoot growth also benefits. A conifer seedling can capitalize on this process if complete or near-complete control of competing vegetation is accomplished during the first few years. After five years, grass can

increase with little risk of a major reduction in conifer growth because the seedlings are normally well established.

Resource managers need a variety of techniques to counteract deleterious vegetation in conifer plantations. Manual techniques, chemicals, grazing animals, fire, and biological controls (grasses replacing shrubs, for example) figure importantly in controlling or eliminating unwanted vegetation. These techniques, used singly or together, are necessary to accomplish the range of biologic and economic objectives of resource managers today.

Biological controls probably will not be as important as the other techniques, overall, but should always be considered and used where possible. Long-term costs may be lower, especially if additional release treatments are not needed. In sensitive areas, biological control may be the only technique available.

Allelopathy, both as an advantage and a disadvantage, should receive increasing consideration in reforestation. It is significant that successful manual, chemical, or animal release treatments often lead to grass understories in young plantations. The effect on conifer growth by chemicals emitted from these grasses could become increasingly important in the near future. Certainly, more information on the allelopathic potential of different grass species in different environments is needed.

The effectiveness of grazing animals to control woody shrubs in young conifer plantations currently is being evaluated. In the past, the general feeling was that grazing animals and young conifer seedlings did not mix. In addition to the papers presented at the International Symposium on "Foothills for Food and Forests" noted earlier, a recent study in northern California (Thomas 1984) indicated that damage from sheep to two- to three-year-old ponderosa pine and Douglas-fir seedlings can be minimal, provided that timing and duration of grazing are closely controlled. Furthermore, controlled grazing seems to favor the establishment of grass and to prohibit new shrubs. Close cooperation between range managers and foresters could mean that young conifer plantations with a combined yield will be more productive because the grasses exclude new shrubs and the animals keep the old shrubs from expanding or producing seeds.

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Sensitivity of Frequency Plots for Detecting Vegetation Change

Abstract

Field procedures that will monitor vegetation changes are required to assess the effects of management activities on rangelands. The more sensitive the monitoring methodology, the earlier any evaluation of management programs may be accomplished.

As a vegetation attribute that can be sampled, frequency has many desirable qualities: it is stable over time, easily measured, and the resulting data is readily analyzed. While frequency is not suitable for vegetation description, it does offer the potential for detecting vegetation change with successive measures over time.

Studies were undertaken to compare the relative sensitivities to vegetational change of three frequency plot sizes (10x25, 15x33.5 and 20x50 cm). The testing was carried out in four different range communities. At each site, frequency of occurrence by species was obtained with each of the frequency plots. Known percentages of vegetation were then excluded from further sampling, thus simulating changes in the vegetation over time. The transect was then resampled. The plot size detecting the smallest amount of change with a given number of samples was deemed to be the most sensitive for a given site.

Results show that each of the frequency plots was very sensitive to successional change. Of the three frequency plot sizes tested, an increase in plot size brought about a corresponding improvement in sensitivity to vegetational change in the particular types of vegetation sampled. In the vegetation sampled in this study, the plot sizes were not large enough to produce frequencies that were less sensitive than the smaller plot sizes.

Introduction

Since effective evaluation of range management programs requires proper assessment of vegetational change, the need for efficient monitoring of range trend has long been recognized (Pickford and Reid 1942, Ellison 1949). Without early detection of trend, it becomes difficult to reverse vegetational change not meeting management goals, since the change is usually well advanced by the time it is detected. In addition, current monitoring techniques often require prohibitively long time spans to note any change due to the implementation of management actions.

Successional trend, as an indicator of change in condition, is expressed by a change in species composition (Costello 1956). This change in composition can be theoretically measured by corresponding changes in cover, yield, density or frequency. However, some of these attributes are more sensitive to successional change than others. For efficient detection of trend, it is preferable to select an easily measured attribute that is sensitive to small changes in species composition, yet insensitive to weather-induced fluctuations. Although cover and yield data are useful in applications such as production studies, they are not desirable for detecting range trend. Seasonal and yearly weather fluctuations greatly affect yield and cover (basal and foliar); hence their levels are too transient for effectively measuring successional change. Density, as opposed to cover and yield, is an essentially stable attribute, particularly with perennial vegetation. Unfortunately, measuring and recording density can be very time consuming, particularly if the plants are small and numerous, or if they reproduce vegetatively (Strickler and Stearns 1963). For these reasons, frequency (species presence or absence) is a more desirable attribute for measuring range trend. Since it is partially determined by density, it is stable over periods of time. In addition, frequency is easily and quickly measured, requiring only species' presence in a plot, and data are readily analyzed statistically (Brown 1954).

Frequency's requirement for different plot sizes according to vegetation type sampled (Kershaw 1973) makes it a poor choice for describing vegetation; it is difficult, without one standardized plot size, to conceptualize frequency

data. However, frequency has the potential for use in trend studies where the data desired represents a difference between two sampling dates rather than a single absolute measurement. Therefore, the objective of this study was to determine if frequency plot data would be more sensitive to detecting small levels of range trend. The greatest benefit of a more sensitive method of measuring trend would be the earlier detection of vegetational change resulting from management practices.

Methods

Field Methods

During the summer of 1981, four sites located within 70 km of Salmon, Idaho, were studied. These sites were selected to test the procedures in a variety of vegetational types. Listed as habitat types (Hironaka *et al.* 1983, Steele *et al.* 1981), the sites are:

1. *Pinus ponderosa/Festuca idahoensis.* Located at an elevation of 1500 m, this site exhibited a typical (Morris and Mowat 1958) fire-maintained *P. ponderosa* stand structure. It combined an uneven-aged stand overstory with a grass-dominated understory.
2. *Artemisia tridentata* subsp. *vaseyana/Festuca idahoensis.* Several *Pseudotsuga menziesii* trees were present on this site, although there was no indication of previous occupation by this species. The elevation was 1975 m.
3. *Artemisia tridentata* subsp. *vaseyana/Festuca idahoensis.* Located at an elevation of 2250 m, this site had been prescribed burned three years prior to sampling.
4. *Artemisia tridentata* subsp. *vaseyana/Festuca idahoensis.* This site was located on an exposed high elevation (2725 m) with an abundance of small forbs and few shrubs. The few *Artemisia* individuals present were small and stunted.

Vegetation data reported in this study consist of the herbaceous component only. Use of scientific names except for *Artemisia* follows Hitchcock and Cronquist (1973).

The sampling process consisted of three phases, designed to simulate trend sampling over a period of years. In phase 1, frequency and cover baseline measurements were taken. Phase 2 consisted of randomly excluding known amounts of vegetation from further sampling, simulating a known compositional change over time. In phase 3, the plots sampled in phase 1 were resampled after the vegetation change had been created. Phases 2 and 3 were completed three times, since three different levels of change were studied.

The sampling unit consisted of a series of successively larger metal plot frames arranged in a nested configuration. The frequency plot sizes were 10x25, 15x33.5, and 20x50 cm, representing areas of 250, 500, and 1000 cm2, respectively. The nested configuration allowed for direct comparison of any one plot size to another, since a plant located in a particular plot would also be included in all plots of a larger size.

At each site, ten 10-m transects were located within a uniform area. The transects were usually placed parallel to each other at a distance of two to three meters. Along each transect, 40 of the nested configurations were uniformly spaced, for a total of 400 samples per site.

At each of the 400 nested configurations, frequency of occurrence for individual species within each of the three frequency plots was recorded. A plant was defined as being present if any portion of the rooted crown occurred within the quadrat. In addition, 120 systematically located point measurements were made along each transect (1200 points per site) to measure foliar cover. These frequency and cover measurements comprise the aforementioned phase 1. Next, phase 2 was conducted. Changes in species number and abundance were created to simulate successional trend. To do this, randomly located sections of the transect, each 20-cm long, were marked off. Each section also extended perpendicularly from the transect 50 cm to include all sizes of the sample plots. Any plant located within these "exclusion areas" was considered to have disappeared, thus simulating a vegetation change over time. To achieve the desired levels of change (10, 20, and 30 percent reduction in vegetation) 5, 10, and 15 exclusion areas, respectively, were located. By superimposing the randomly located exclusion areas over the uniformly spaced sample plots, varying amounts of vegetation change within a single sample plot could be created, from complete exclusion to no change. Neither of these extremes occurred frequently. Instead, varying

amounts of partial overlap occurred between the sample plots and the exclusion areas. Following each of the three levels of change, phase 3 was accomplished by resampling the original sample plots and the exclusion areas. Following each of the three levels of change, phase 3 was accomplished by resampling the original sample plots, minus the exclusion areas, for frequency and cover.

In summary, the field sampling consisted of:

1. a) recording the initial frequency data for the three plots within each of the 400 concentric configurations per site;
   b) recording foliar cover generated by 1200 points per site;
2. creating a change in the vegetation;
3. resampling the original frequency plots and cover points after the change had been made.

Steps 2 and 3 were done three times, once at each level of change introduced (10, 20, and 30 percent). While this study considered "change" to be a reduction in species variety and abundance, a reversal of the data could be used to discuss the effects of species increase. With the same set of data, however, the results of an increase were not tested. Since this study was testing various plot sizes for sensitivity to small levels of change, the amount of change induced was limited to a maximum of 30 percent.

The objective of this study was to compare changes in frequency levels detected by different plot sizes. Without a reference standard, it would be impossible to determine if the frequency changes detected by one plot size were more precise than any other plot size. Frequency itself could not be used as a reference for two reasons: 1) it is the value being tested, and 2) its results are highly related to plot size. For these reasons a vegetation measurement other than frequency had to be established as a reference. Density, yield and cover were considered. For practical reasons, cover was the attribute chosen. It was found, however, that basal cover levels at the sites studied, were too small to be useful. Foliar cover was thus chosen as the reference standard. It was determined that sampling foliar cover at such an intensive level (1200 points per site), would give an accurate assessment of change (Table 1). The sole purpose of the foliar cover data was to determine whether a significant vegetation change had occurred as a result of the exclusion process. No attempt was made to relate cover to frequency. Normally, foliar cover is not used to determine trend; it is subject to yearly and seasonal environmental fluctuations. However, it was used as a parameter in this study since all sampling on a site was done in a few days' time, during which vegetation changes were insignificant.

TABLE 1. Percent foliar cover before and after each exclusion level, high elevation *Artemisia tridentata* subsp. *vaseyana/Festuca idahoensis* habitat type.

Exclusion Level (%)	Foliar Cover	Percent Change in Foliar Cover From Original (0% Exclusion) Level
0	38	
10	34	10
20	31	18*
30	28	26**

*Significant at the alpha = 0.20
**Significant at the alpha = 0.10
Significance determined by separate 't' test between the control level and each of the three "exclusion" levels.

Data Analysis

Sampling 400 plots is usually considered to be too time consuming for most management requirements. Therefore, to enhance the usefulness of this study, the original 400 nested configurations were considered to be a population, from which a random sample of 200 was drawn. The 600 foliar cover points associated with these 200 samples were also used in the analysis. All results shown here are from the smaller (200) sample size. Data from each of the four sites were analyzed independently; no attempt was made to combine information from different sites.

Individual 't' tests were used with the foliar cover data to determine, as a reference standard, if the exclusion process had indeed made significant changes in the vegetation. With alpha = 0.10 or 0.20, tests were made on differences in percent foliar cover between the control (original) level and each of the three separate "exclusion levels." Each of the 10 transects (40 nested configurations each) within a site was considered a sample.

A Chi-square test with Yates' correction factor (Mueller-Dombois and Ellenberg 1974) was

used to determine, for each plot size, if significant changes in frequency had occurred between the control and any of the exclusion levels. The data used in these tests were the number of occurrences of each species per plot size at the control and each "exclusion level." With the total number of samples taken also known, the frequency data were arranged in a presence-absence form, utilized in the Chi-square analysis. For all species, the number of occurrences in each plot size at the control level was tested against the three exclusion levels. For the Chi-square test, each species-plot size combination was considered a sample. Results were compared at alpha levels of 0.20 and 0.10.

While placing the three plot sizes in a nested arrangement helps ensure that any plants found in a given plot size are subsequently located in all larger plot sizes, statistical comparisons between plot sizes would be inappropriate, since the nesting procedure violates the rule of independence.

Results and Discussion

Foliar Cover

Except as noted, only the results from the exposed high elevation *Artemisia tridentata* subsp. *vaseyana/Festuca idahoensis* habitat type will be reported. Results from the other three sites are similar to this one, and are being excluded only for brevity.

Results of the separate t-test procedures using the foliar cover data from the *Artemisia tridentata* subsp. *Vaseyana/Festuca idahoensis* showed the following: It was not possible to detect a significant difference (alpha = 0.20) in foliar cover when only 10 percent of the vegetation was excluded (Table 1). However, at the 20 percent "exclusion level," a statistical (alpha = 0.20) difference in foliar cover was noted. After 30 percent of the vegetation was excluded, a statistically valid change (alpha = 0.10) occurred when compared to the control level. Considering the intensity of the foliar cover sampling, this information provides a standard against which the frequency data can be compared; without the foliar cover results, it would be impossible to validate the frequency results. In addition, at all sites, the percent changes in foliar cover from the control levels nearly equalled the percent changes made based on the exclusion level (Table 1).

Frequency

The results of the Chi-square test on species occurrence are shown in Table 2. It is apparent that two factors are interacting to determine if a given plot size can detect a change in any species. One factor is the initial frequency of the species, the other is the magnitude of change in frequency. To further reveal these effects on detecting trend, the lowest level at which a change in species frequency became significant (alpha = 0.20 or 0.10) in any plot size is plotted against the control frequency level (Fig. 1). This graph shows that in order to detect a relatively small change in species occurrence, there had to be a large initial frequency value. With smaller initial frequency values, it was more difficult for the frequency plots to detect small changes in the vegetation. Therefore, to detect as small a change in the vegetation as possible, a plot size must be used that will give optimum frequency values. Curtis and McIntosh (1950) state that for frequency sampling, plot size should be adjusted so that the most prevalent species receives a frequency value of 63 to 86 percent. This study supports that view. Additionally, for trend detection, plot sizes that give higher frequency values than these should be avoided. If a species becomes more prevalent over time to the point where it reaches 100 percent frequency, its usefulness for detecting change is lost, since at this level, there is no way to compare relative differences with previous values. Figure 1 also shows that as an increasing amount of change is created, the frequency plots become more effective at detecting that change; detection of large changes in the vegetation can be accomplished with smaller initial frequencies.

This study noted several other interrelated points. First, as would be expected, plot size was positively correlated with frequency. Thus frequency, in turn (along with the magnitude of change), determined the sensitivity of that plot size to detecting change. The largest plot size tested was generally most sensitive to detecting change in the vegetation, due to the optimum frequency values it provided.

Second, the largest plot size tested usually showed a change in a larger number of species than did the smaller plot sizes. These additional species are important, since they improve the sensitivity of detecting change in species composition.

TABLE 2. Results of the Chi-square analysis on frequency for the *Artemisia tridentata* subsp. *vaseyana/Festuca idahoensis* habitat type. The first row for each plot size contains the initial frequency and the three subsequent frequencies resulting from the exclusion process. The second row is the percent change from that original frequency. This list includes only species in which a change was detected.

Species	Initial cover (%)	Plot size	Exclusion Level (%) 0	10	20	30
Phlox multiflora	7.8	10x25	62	58	54	47
				6	13*	24**
		15x33.5	82	79	72	66
				5	12**	20**
		20x50	90	87	83	79
				3	8**	12**
Festuca idahoensis	7.5	10x25	64	60	55	52
				6	14**	19**
		15x33.5	87	82	78	73
				6*	10**	16**
		20x50	95	92	90	86
				3	5**	9**
Antennaria microphylla	4.7	10x25	60	56	52	48
				7	13*	20**
		15x33.5	77	72	67	62
				6	13**	19**
		20x50	86	82	78	74
				5	9**	14**
Agoseris glauca	3.2	10x25	42	37	35	31
				12	17	26**
		15x33.5	53	50	47	43
				6	11	19*
		20x50	62	58	56	51
				6	10	18**
Poa sandbergii	2.0	10x25	36	34	32	30
				6	11	17*
		15x33.5	52	48	45	41
				8	13	21**
		20x50	68	63	60	56
				7	11*	18**
Carex xerantica	1.7	10x25	18	16	15	14
				11	17	22
		15x33.5	28	25	24	21
				11	14	25*
		20x50	38	36	34	31
				5	11	18
Arnica sororia	1.5	10x25	36	30	28	25
				17	22*	31**
		15x33.5	48	44	41	39
				8	15	19*
		20x50	63	58	55	52
				8	13*	17**
Erigeron compositus	1.2	10x25	30	28	27	24
				7	10	20*
		15x33.5	39	36	34	32
				8	13	18*
		20x50	50	47	46	42
				6	8	16*

TABLE 2 continued.

Species	Initial cover (%)	Plot size	Exclusion Level (%) 0	10	20	30
Arenaria congesta	1.2	10x25	46	43	39	36
				6	15*	22**
		15x33.5	66	60	56	54
				9	15**	18**
		20x50	77	72	68	67
				6	12**	13**
Eriogonum acuminata	1.0	10x25	20	18	16	13
				10	20	35*
		15x33.5	29	26	25	23
				10	14	21
		20x50	44	41	38	37
				7	14	16*
Phlox longifolia	0.7	10x25	26	23	20	18
				12	23	31**
		15x33.5	34	30	28	26
				12	18	24*
		20x50	46	42	40	38
				9	13	17*
Draba densifolia	0.2	10x25	13	12	11	9
				8	15	31
		15x33.5	22	20	18	14
				9	18	36**
		20x50	33	32	30	26
				3	9	21*

*Significant at alpha = 0.20
**Significant at alpha = 0.10

Third, with only one exception, a change created by excluding 10 percent of the plants along the transect could not be detected by any of the frequency plot sizes. When exclusion levels reached 20 and 30 percent, the resulting changes in frequency could regularly be detected, especially with the larger plot sizes. Examination of Figure 1 can provide estimations, for those sites studied, of the minimum initial frequencies needed to detect a particular change in frequency. For example, at this site (a high elevation *A. tridentata* subsp. *vaseyana/F. idahoensis* habitat type), a plot size providing an initial frequency of at least 60 percent would be necessary to detect a subsequent 15 percent change in frequency. This figure also shows that it was difficult for any single frequency plot, of the sizes tested, to consistently detect changes in frequency less than about 10 percent. As the change became greater than 10 percent, frequency plots became quite useful for detecting that change.

Fourth, the species in Table 2 have been listed in descending order of initial (control) foliar cover. This was done to illustrate that foliar cover can be used as a guide for determining which species might be abundant enough to show significant changes when using frequency to detect trend. This is not to imply that there are direct relationships between frequency and cover. It is, however, very difficult to determine before sampling what a species' frequency will be. Simple ocular estimation of foliar cover can provide the land manager with a rough estimate of the various species' abundance and of the frequency plot sizes which might be successfully used on a given site for trend analysis. For example, on all sites, it was difficult to consistently detect trend, using frequency, in any species with an initial foliar cover less than about one or two percent. If management needs were considered for these four particular sites, frequency sampling of species with foliar covers less than about one

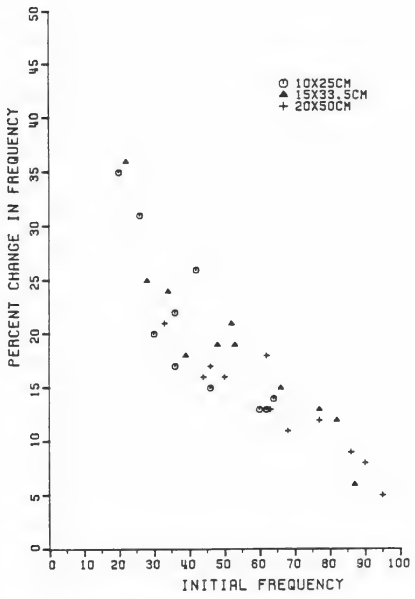

Figure 1. Initial frequency versus the smallest significant (alpha = 0.20 or 0.10) percent change detected at any exclusion level, by plot size, (*Artemisia tridentata* subsp. *vaseyana/Festuca idahoensis* habitat type).

or two percent might not provide much additional information. Additionally, this level is a crude approximation and applies only to those sites covered in this study. There are, however, situations where this foliar cover generalization might not hold true. Species with large spreading leaves and small bases would tend to have high foliar cover levels, yet low frequency levels. Since the Chi-square analysis is based on species presence-absence, one would not expect the small frequency levels, in these cases, to be sensitive to change for such species with large foliar and small basal cover.

In summary, the specific results for the *Artemisia tridentata* subsp. *vaseyana/Festuca idahoensis* habitat type are as follows. Density and dispersion characteristics combined to create high frequency levels. As a result, 12 of the 22 species found at this site reflected a statistical change (Table 2). Initial frequencies of any plot size-species combination showing a significant difference varied from 22 to 95 percent. At this site, either the 15x33.5-cm or 20x50-cm plot would be adequate for detecting small changes in the vegetation. They both detected about the same change (six and five percent, respectively), and they detected differences in the same number of species (11). This similarity is most likely due to the high frequency readings that both plot sizes developed. Although the 10x25-cm plot detected differences in a large number of species (10), the smallest change it could detect was 13 percent, more than twice that of either the 15x33.5-cm or 20x50-cm plots.

Conclusions

At four sites in Idaho, 10x25, 15x33.5, and 20x50-cm frequency plots were sensitive to known changes in the vegetation. Each of these larger frequency plots regularly detected small amounts of vegetation change at alpha = 0.20 and 0.10.

Initial frequency as well as the magnitude of change in frequency are primarily responsible for determining sensitivity to vegetational change. Those plot sizes giving higher initial frequency readings were more sensitive to detecting subsequent changes in frequency. The number of species in which a significant change was detected was positively related to plot size.

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RESEARCH NEWS AND COMMENTS

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Ecology and Environmental Problem-Solving

Introduction

Most important environmental problems are complex, and we lack components of knowledge that would be helpful in designing creative approaches to those problems. But difficulties in environmental planning can arise not only from a lack of information. Often, available knowledge is not used fully during environmental problem-solving exercises. Failure to use existing information results from a variety of causes. Problem solvers may be unaware of the existence of potentially valuable information; people who are aware of potentially valuable information may not sense its importance because they think of it in a basic scientific context rather than an applied one; time constraints often prevent a thorough literature search.

A new book sets out to address these problems in relation to the management and control of environmental effects of human activities. Specifically, the book focuses upon practical ways to both expand our knowledge base and use available information more effectively in dealing with environmental problems. The book is a publication of the National Academy of Sciences/National Research Council (NAS 1986).[1] It is a product of several years of work by a committee of nine basic and applied ecologists, assisted by a consultant and an NAS staff officer. It deals first with protocols that should increase the probability that available information will enter into problem solving activities. This is covered specifically in a Chapter on "A Scientific Framework for Environmental Problem-Solving" which points to the value of thinking before acting and using established scientific principles. This idea has been expressed a number of times in recent years (Andrews *et al.* 1977, Council on Environmental Quality 1978, Fritz *et al.* 1980, Holling 1978, Rosenberg *et al.* 1981, Larkin 1984, Sanders *et al.* 1980, Sharma *et al.* 1976, States *et al.* 1978, Walters 1986, Ward 1978), and developed extensively in a recent Canadian review of the issue (Beanlands and Duinker 1983). Secondly, the book deals with ways in which both basic and applied ecologists can better perceive the value of ecological knowledge for dealing with different problem-solving arenas.

Recommendations

As articulated in the NAS document, the foundations of a sound framework for approaching and devising solutions to environmental problems should contain the following features.

Involve Scientists from the Beginning

Scientists have no special expertise in determining societal goals and values, but they do have knowledge that is important for identifying those components of affected ecosystems of special value from a functional, dynamic perspective. In particular, they may know which organisms have important functional roles in ecosystems that are not generally appreciated by the public at large. Scientists are also likely to be familiar with the results of similar projects elsewhere. Their experience allows them to advise decision-makers on the probable costs of making the measurements necessary to evaluate different options.

[1] *Ecological Knowledge and Environmental Problem-Solving*, available from the National Academy Press, 2101 Constitution Avenue, N.W., Washington, D.C. 20418. Price $24.50.

Appropriate Boundaries in Space and Time

The knowledge of scientists is especially important in assessing how far in space and time the influences of a particular project are likely to be felt. By bounding a project, attention can be directed toward studying the key processes in those places where the effects of the project are likely to be the strongest. For example, aquatic effects are normally bounded by watersheds and tend to be concentrated at river mouths and estuaries, whereas air pollution problems tend to be widely dispersed. Also, establishing boundaries helps to identify situations in which effects will cross important political boundaries. This process helps to identify all groups that need to be involved in planning for and advising on the desirability of a project.

Consider Cumulative Effects

It is important to view individual projects in the context of other similar activities. Small projects, even if they are individually trivial, can have important cumulative effects if they are repeated in space and time. Filling in a small part of an estuary may not, in itself, be environmentally significant, but many small fills are almost certain to be. Indeed, one of the most important cumulative effects is the gradual "nibbling away" of habitat types by small projects, no one of which would be judged to have major impacts (Beanlands *et al.* 1986).

Allow for Uncertainty

There are serious gaps in the scientific knowledge base available to be applied to environmental problem-solving, and there are many unpredictable variations in natural ecosystems. No amount of scientific effort will suffice to make the art of predicting impacts of environmental perturbations a precise one. Therefore, all planners and managers should expect surprises and plan accordingly. This process is called Adaptive Environmental Management (Holling 1978) because the total plan is not established at the beginning. Rather, the first steps are taken, evaluated, and the plan is then modified as a result of the information gained.

Treat Projects as Experiments

Rather than viewing the environmental impact assessment requirement as a legal hurdle, either to be overcome or to be used to attempt to block projects, this valuable process should be viewed as an opportunity to learn scientific and management lessons. Most projects for which environmental impact statements are prepared, as well as many other activities affecting the environment, are on a scale larger than is normally feasible with typical scientific experiments. Accordingly, they provide our only opportunities to test empirically the effects of many types of perturbations on the functioning of ecological systems. In addition, many types of projects, such as power plants, dams, and roads are often repeated in basically the same form. By treating each project as an experiment we can be in a better position to evaluate the effects of subsequent ones and to direct attention to those components whose intensive study will be most informative for understanding other projects. An essential part of treating projects as experiments is a carefully designed monitoring program that is started before the project begins and which continues for an appropriate length of time after the project is completed. To be most effective, the design of the monitoring program should be built into the study plans early in the planning process.

These components are, of course, the basic ingredients of all good scientific research. It is, however, much easier to incorporate them into scientific projects because papers lacking them will not be accepted for publication in the standard journals. Environmental impact statements are, on the other hand, evaluated in the courtroom rather than by a peer review system. Moreover, the goals of the evaluators usually are not to assess objectively the underlying science, but rather to muster arguments either for or against a project. One of the consequences is that both proponents and opponents of projects tend to lose interest in the actual impacts once a project is approved. The proponents would prefer not to know what the impacts really are, and opponents shift their attention to other projects in an attempt to block them. These motives are likely to remain in force for some time, making it difficult to implement fully a procedure of treating projects as experiments. Nonetheless, if, as a society, we are truly interested in improving the means by which we assess the impacts of projects so that their potential benefits can be realized while adverse impacts on the environment are minimized, it is necessary to move in that direction.

Case Studies

Appropriate application of existing scientific information does not guarantee correct predictions because ecological systems are complex, each situation is unique, and the predictive powers of current ecological theories are inadequate. Nevertheless, even inaccurate predictions are better than none because the nature of our failures help to reveal the limits of current knowledge and may indicate where better theoretical developments are most urgently needed. In addition, use of available knowledge can and does improve environmental problem-solving. The NAS volume *Ecological Knowledge and Environmental Problem-solving* discusses thirteen case studies in which ecological knowledge was successfully applied to environmental problem-solving. These case studies were selected to cover a broad array of types of environmental problem-solving. Some cases, such as those of the North Pacific Halibut, the Spotted Owl, and Newfoundland Caribou, involved protection of a single species or achievement of a long-term sustainable harvest. In other cases, such as the Garki Malaria Project, California Red Scale, and Vampire Bat case studies, the objective was to eliminate an organism, or at least to reduce it enough to render it economically insignificant. These projects drew heavily on life history theory and depended importantly on knowing the natural history of the focal organisms. For example, the fact that Vampire Bats mutually groom one another offered the key to a control method of placing poison on the fur of a few individuals and allowing the bats themselves to spread the poison to a much larger number of individuals. This method, which affected only the target species, was much more successful and environmentally sensitive than the previously tried methods which had included dynamiting caves in which the bats, and other organisms, roosted.

Other case studies deal with community-level problems. Among the objectives of these projects were achievement of sustained steady yield of useful forest products (the New Brunswick forest case study), and the restoration of a complex ecological community similar to the one that existed prior to the human-induced perturbations. In the Lake Washington case study, scientific information on the functioning of the lake, combined with knowledge of changes occurring in other temperate zone lakes receiving municipal waste discharges, was vital in convincing political leaders to undertake the costly and politically risky enterprise of eliminating sewage discharges to the lake by means of construction of a collection system encompassing many municipalities. In this case, the predictions of the effects of eliminating discharges into the lake were verified by monitoring the lake during its recovery.

Scientific information was less successful in predicting the effects of a dam constructed on Southern Indian Lake in Manitoba, Canada. Scientists studying Southern Indian Lake utilized nearly all the sources of available ecological knowledge, but they were hampered by the fact that no information was available from other large, shallow lakes in subarctic regions underlain by permafrost. Shoreline erosion and liberation of mercury into the water was more extensive than predicted, and the important native whitefish fishery was negatively impacted in ways that were unanticipated. Nonetheless, as a result of the careful scientific studies done on Southern Indian Lake, we are in a much better position to predict changes in other subarctic lakes if their levels are raised.

Reclamation of land left in a derelict or otherwise undesirable state is a rapidly developing component of applied ecology. The art is best developed in Britain where pressures on the land are intense. Early reclamation attempts merely tried to produce vegetation that looked pleasing and reduced soil erosion. Today, rising ecological consciousness has resulted in societal demands that more complex natural communities of plants and animals be restored. Successful restoration of such communities depends upon knowledge of the tolerances of different plant species for environmental conditions; the way in which they compete for water, light, and mineral resources; and the way these interactions combine to produce patterns of vegetation succession. The Longstone Edge Project in Derbyshire, England, represents the current state-of-the-art in land reclamation. In addition, the project drew upon and contributed to the development of new ideas about plant competition and succession. Investigators devised pilot experiments to develop more powerful predictive theories for revegetation of the types of landscape represented by the abandoned mine at Longstone Edge. An excellent

summary of knowledge and experience in Britain with land restoration is provided by Bradshaw and Chadwick (1980).

Still other case studies deal with projects whose goals were to determine the impacts of activities that take place in many locations over broad areas. The NAS report discusses the use of DDT in the United States, effects of forest clearcutting on nutrient cycles, and the effects of nuclear radiation on biological communities.

Common Themes

In combination, the case studies reveal a great deal about the strengths of ecological knowledge when properly applied to environmental problem-solving and the limitations on its current use. Running through the case studies are the following common themes that derive from basic characteristics of ecological systems.

Important Effects are Often Indirect

The obvious and direct influences on the objects of study are sometimes not as important as less obvious, indirect effects. In the DDT case, for example, the indirect effects on top carnivores, often thousands of miles away from the sites of application of the pesticide, were very important. They were the result of biological concentration of the chemical and its high mobility in the atmosphere, and they were quite unexpected at the time. They are today, however, predictable consequences of the use of pesticides with the properties of DDT. Similarly, in Southern Indian Lake, the mobilization of mercury as a result of erosion of banks by the rising waters of the lake, was a major indirect effect on biological communities in the lake.

Density-dependence

Usually, conditions deteriorate for individuals as the density of individuals of the same species, their predators, and their parasites increase. Conversely, conditions usually improve when the numbers of individuals in those groups decrease. Therefore, survival and reproductive rates in populations are usually sensitive to changes in density, even though those changes are seldom simple, direct, or readily predictable. Density dependence is basic to such management practices as design of optimal harvesting levels, biological control, and management of rare and endangered species.

Individual Uniqueness

Sexually reproducing populations are composed of individuals differing in their age, sex, physiological condition, and genotype. Organisms with modular growth, such as plants and many sessile marine invertebrates, often have substantial intraindividual variability that is important for consumers of those organisms (Whittam *et al.* 1984). Management practices often create selective pressures that cause genetic and, hence, phenotypic changes in a population that may act to thwart the goals of management practices. The evolution of resistance to biocides is a striking case in point.

Fragmentation

Populations divided into isolated or semi-isolated subpopulations may behave very differently than populations with relatively continuous distributions over large areas. Human activities often change large patches of vegetation of one type, a forest or prairie, into small patches surrounded by land devoted to other purposes. Such fragmentation of habitats sets into motion processes that cause important changes. Species unable to exist in small patches may go extinct. Even species that can adapt to small patches may not be present in most of them because immigration rates into isolated units are lower than extinction rates in them. Local populations are vulnerable to extinction by events affecting specific areas. If such local extinctions do occur, rates of recolonization are likely to be directly related to the degree of isolation of the patches. Fragmentation of habitats is one of the most important cumulative effects of human activities.

Scaling

Ecological problems are expressed in very different scales in space and time. Large lakes are not simply small lakes made bigger. A large expanse of forest is not the same as a collection of small woodlots. Patchy environments have more edges in proportion to their area than do homogeneous environments. Speciation of larger organisms requires large expanses of suitable habitats (Soulé and Wilcox 1980). In time, the effects of perturbations may be noticed

immediately in communities dominated by short-lived individuals, but a forest may maintain itself for many decades even if reproduction of the dominant members of the canopy has been suppressed. Among short-lived organisms, evolutionary changes may occur rapidly enough to change their responses to the perturbations and affect the entire dynamics of the system. Understanding which effects are manifest at which spatial and temporal scales is vital to effective scoping of environmental problems.

Conclusions

It has been argued that much of the effort devoted to the preparation, reading (if indeed they are read), and debating of environmental impact statements is wasted (Goodman 1975, Schindler 1976, Suter 1981). There is much to be said for this charge. Much irrelevant or useless information is compiled in EISs, and it is commonplace that existing information that would be genuinely useful to projects is not gathered and incorporated into planning for them. Nonetheless, the legal requirement to prepare EISs is an important achievement because it signals our recognition as a society of our dependence upon the functioning of ecological systems that are easily abused. Our objective in the future should be to utilize the opportunity provided by the requirement to evaluate environmental effects of our actions to learn how our activities change the functioning of ecosystems. There are enough examples where a serious attempt to adopt a scientific approach to environmental problem-solving resulted in improved practices to indicate that we have just begun to exploit the possibilities of approaches to environmental problem-solving that use what we already know and generate new knowledge for the future.

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